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PRIMARY PRODUCTION OF SALT-MARSH COMMUNITIES ON THE ISLAND OF TERSCHELLING IN THE NETHERLANDS

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Promotor: Prof.Dr. V. Westhoff

Dit proefschrift zal tevens verschijnen in de reeks Verhandelingen van het Rijksinstituut voor Natuurbeheer.

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PRIMARY PRODUCTION OF SALT-MARSH COMMUNITIES ON THE ISLAND OF TERSCHELLING IN THE NETHERLANDS

PROEFSCHRIFT

TER VERKRIJGING VAN DE GRAAD VAN DOCTOR
IN DE WISKUNDE EN NATUURWETENSCHAPPEN
AAN DE KATHOLIEKE UNIVERSITEIT TE NIJMEGEN,
OP GEZAG VAN DE RECTOR MAGNIFICUS,
DR. G. BRENNINKMEIJER,
HOOGLERAAR IN DE FACULTEIT
DER SOCIALE WETENSCHAPPEN,
VOLGENS BESLUIT VAN DE SENAAT
IN HET OPENBAAR TE VERDEDIGEN
OP VRIJDAG 22 SEPTEMBER 1972
DES NAMIDDAGS TE 2 UUR PRECIES

DOOR

PIETER KETNER

GEBOREN TE AMSTERDAM

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THOBEN OFFSET NIJMEGEN

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I

INTRODUCTION AND SCOPE OF THE INVESTIGATIONS

The research discussed in this publication, concerning the primary production of salt-marshes, was carried out within the framework of the International Biological Programme, section PT (IBP/PT, see Hekstra, 1965; Montalenti, 1966). This IBP, after years of preparation, was proposed by the International Council of Scientific Unions as follows: 'As a result of the rapid rate of increase in the numbers and needs of the human populations of the world, and their demands on the natural environments, there is an urgent need for strengthened biological research'. The main title of the whole programme reads: 'The Biological Basis of Productivity and Human Welfare' (IBP News Nos. 1 & 2, 1964, 1965; Hekstra, 1965; Montalenti, 1966). Of the 7 sections, into which IBP is devided, section PT (Productivity Terrestrial) embraces the field of research of the production, primary as well as secondary, of terrestrial ecosystems (IBP News No.9, 1967).

The primary productivity (production) of an ecosystem can be defined as: 'the rate at which energy is stored by photosynthetic and chemosynthetic organisms (chiefly green plants), in the form of organic substances which can be used as food materials' (Odum, 1959, 1971). A distinction must be made here between the gross primary production and the net primary production. The gross primary production (total assimilation or total photosynthesis) is the total photosynthesis, including the organic matter used for respiration of the producing organisms during the measurement period. The net primary production (net assimilation or apparent photosynthesis) is the gross primary production minus the energy used for respiration (cf. Odum, 1959, 1963, 1971; Anon, 1966); or alternatively 'the net primary production is the biomass which is incorporated into a plant community during a specified time interval, less that required for respiration' (Milner & Hughes, 1968). The secondary production is the production of material by organisms (consumers) which live from the producers. For more definitions of terms applied in the production investigations, readers are referred to MacFadyan, 1948; Westlake, 1963; Anonymous, 1966; IBP News No.10, 1968; Milner & Hughes, 1968; Odum, 1971.

After the Royal Netherlands Academy of Sciences had decided that the

Netherlands should take part in the IBP (1964), the former State Institute for Nature Conservation Research (now the Research Institute for Nature Management dept. Leersum), was asked to propose a programme within the scope of the PT section, concerning the investigations which could be undertaken in the Netherlands and the area in which they had to be carried out. In choosing the experimental sites, the requirements laid down by the Special IBP Committee should be taken into account.

On the advice of the above mentioned Institute it was proposed to direct the investigations towards:

1. salt-marshes, under the auspices of the State Institute for Nature Conservation Research;
2. forests, under the auspices of the Institute for Biological Field Research (now Research Institute for Nature Management, dept. Arnhem);
3. reed swamps, under the auspices of the Laboratory for Plant Ecology in Groningen.

Only the first mentioned subject will be dealt with in this study.

The salt-marshes of the State Nature Reserve Boschplaat were chosen for investigation. The Boschplaat can be considered as one of the few large areas in the Netherlands with a so-called sub-natural landscape. 'In a sub-natural landscape the flora and fauna are native and spontaneous, although there may be some minor exceptions. The basic vegetation appearance and structure are not quite undisturbed; they have to a certain extent been influenced by man. But they are closely related to the potential natural vegetation, belong to the same formation type as the original landscape, and share the latter's physiognomy.' (Westhoff, 1971c) In this way it differs from the natural landscape (no longer existing in Western and Central Europe), where the flora and fauna are native and spontaneous and the vegetation undisturbed by man, as well as from the semi-natural and cultivated landscapes. In semi-natural landscapes the flora and fauna are completely, or for the greater part, spontaneous, but the vegetation appearance is determined by man and deviates strongly from that which would be present under natural conditions; in cultivated landscapes the composition of the flora and fauna and the vegetation appearance are totally, or for the greater part, determined by man (see Westhoff, 1949, 1952, 1968, 1970, 1971a, b and c).

The frequently used but often undefined term in Anglo-American literature 'natural vegetation' or 'natural community' usually refers indiscriminately to the vegetation in natural, sub-natural or semi-natural landscapes. In the present study the term 'natural vegetation' will be used in this more general sense.

The fact that the natural grasslands in the humid climate of Western Europe are almost always limited to salt-marshes, played an important role in the choice of the area to be studied. Other determining factors were that grazed as

well as ungrazed vegetations, which from an abiotic point of view belong to similar ecosystems, occur next to each other on the Boschplaat, and that salt-marsh vegetations, as a result of reclamation, are becoming more rare.

In the years 1967-1971 the primary production was determined from three vegetations, two of which were ungrazed and the other grazed. Several facets of the secondary production were also studied by other investigators. The results of these studies will be published elsewhere. The problems in the research concerning the primary production were formulated as follows:

How are the plant communities composed and how much organic material, above ground (stems, leaves and flowering stalks) as well as underground (roots, rhizomes), is produced periodically by these vegetations?

How large are the variations in production per vegetation between the different years, and how great are the differences in production between the various vegetations?

Can these differences be connected with those observed in some abiotic factors?

How great is the rate of decay of the dead plant material?

How great is the efficiency in the use of solar energy by the vegetations?

Although much phyto-sociological and ecological research has been carried out on salt-marsh vegetations (see Westhoff, 1947; Chapman, 1960; Beeftink, 1965, 1966, 1968; and the references therein, and further Adams, 1963; Bolen, 1964; Miyawaki & Ohba, 1965; Vogl, 1966; Blum, 1968; Taylor & Burrows, 1968; Hubbard & Stebbings, 1968; Teal, 1969; Westhoff & Den Held, 1969; Hubbard, 1970; Boorman, 1971; Brereton, 1971; Tüxen, 1971), production data about these vegetations are scarce. Happer (1918), Odum & Smalley (1957) and Smalley (1959) determined the production of Spartina alterniflora in Georgia. Teal (1959, 1962) used Smalley's data for the calculation of the total energy flow in a salt-marsh ecosystem. Ranwell (1961, 1964a; Ranwell et al., 1964) give a few production figures for grazed and ungrazed salt-marshes in England.

Before the IBP existed, research was already being carried out into the production of natural grasslands, grazed as well as ungrazed (in America: Tomanek & Albertson, 1957; Blaisdell, 1958; Bray, Lawrence & Pearson, 1959; Golley, 1960; Odum, 1960; Bray, 1962; Ovington, Heitkamp & Lawrence, 1963; Wiegert & Evans, 1964; Pearson, 1965; in Europe: Pearsall & Gorham 1956; Hughes, 1958; Krause, 1960; Rawes, 1963; Welch & Rawes, 1965; Rawes & Welch, 1966). All these investigations are related to dry grasslands, in America mostly on prairies or on so-called old fields (i.e. former croplands).

A few investigators have also studied root production (Bray et al., 1959; Schuster, 1964; Wiegert & Evans, 1964; Pearson, 1965).

During the last few years, and through the medium of the IBP, interest in

production-ecological research has greatly increased (Sukachev & Dylis, 1966; Kucera et al., 1967; Menhinick, 1967; Williams, 1968; Moir, 1969; Kelly et al., 1969; Old, 1969; Numata, 1970) and many teams are involved within the framework of this programme (see detailed list of the IBP projects in IBP News No.13, 1969). A survey of the IBP grasslands projects is given by Coupland & Van Dyne (1970).

Only a small number of these IBP projects (e.g. America, Canada, Japan) are studying the total grassland ecosystem, that is to say the producers as well as all the consumers and reducers, in connection with abiotic factors. The majority of the projects concerns facets of the primary and/or secondary production.

Although a few IBP/PT grassland projects were started as far back as 1964, only very few results have been published to date (Medwecka-Kornaś, 1967; Kotańska, 1967; Jakrlová, 1968, 1971; Traczyk, 1968, 1971; Kosonen, 1969; Ellenberg, 1971). Preliminary results appear in Annual Reports of the projects concerned and in various Progress Reports from the national IBP Committees. It is the intention that all IBP grassland data will be collected in one Institute and processed and compared with each other there.

This publication must therefore be seen as an interim report, in which as many data as possible have been collected, as desired within the framework of the IBP (see IBP News No.9, 1967), but in which it has not yet been possible to compare these data with those of other investigators. As a result of this, the synthesis of the data presented in this publication has not yet been processed in full.

The nomenclature of the species in this study is according to Heukels-Van Ooststroom (1970). For the infraspecific taxa – not mentioned by Heukels-Van Ooststroom – the reader is referred to Beeftink (1965) and Westhoff & Den Held (1969).

GENERAL FEATURES OF THE INVESTIGATED AREA

Site description

The State Nature Reserve the Boschplaat occupies the eastern part of the island of Terschelling, one of the West Frisian islands in the north of the Netherlands (53° 22′ N., 5° 13′ E; see fig.1). The length of the region is almost 10 km. The surface area amounts to ± 4400 ha, measured according to the low-water line; at an average high-tide the surface is ± 2950 ha, while ± 85% of the ± 4400 ha can become submerged during very high-tides (Westhoff, 1951).

Originally the Boschplaat consisted of a sandy plain containing a few small dunes, seperated from Terschelling by a tidal inlet the 'Koggediep'. This inlet sanded up after 1750 and the so-called Koggegronden ('Kogge lands') came into existence with connected the sandy plain to the islands at low-tide. Until 1930 there was hardly any vegetation except for on and around the row of dune islands on the southern side of the plain, the so-called Eerste Duintjes, Tweede Duintjes, Derde Duintjes, Vierde Duintjes and the Amelander Duin ('First, Second, Third and Fourth Little Dunes and the Amelander Dune'). During high-tide the plain was still regularly submerged (Westhoff, 1947; Westhoff & Brouwer, 1951).

Between 1929-1931 attempts were made to narrow the connection between the Wadden Sea and the North Sea by constructing a sand dam from the north-eastern point of the main island to the First Little Dunes. This semi-natural dike, which was meant to grow higher by aeoloan accumulation of sand, burst in 1931, apparently due to the fact that the dike was not in a good position with regard to the prevailing wind. From 1931-1937 a similar dike (the so-called 'Stuifdijk') was constructed, this time in a more northerly direction. This stretches even today over the whole length of the Boschplaat north of the row of Little Dunes from km mark 20 to km mark 29 (Visser, 1947). The old dike, which now came to lie in the lee of the new dike, has not increased any more but is still to be seen. The break has widened into a gap having a breadth of ± 175 m. Since this Stuifdijk was formed, the Boschplaat can only be flooded from the Wadden Sea and during this flooding silt is deposited. Major

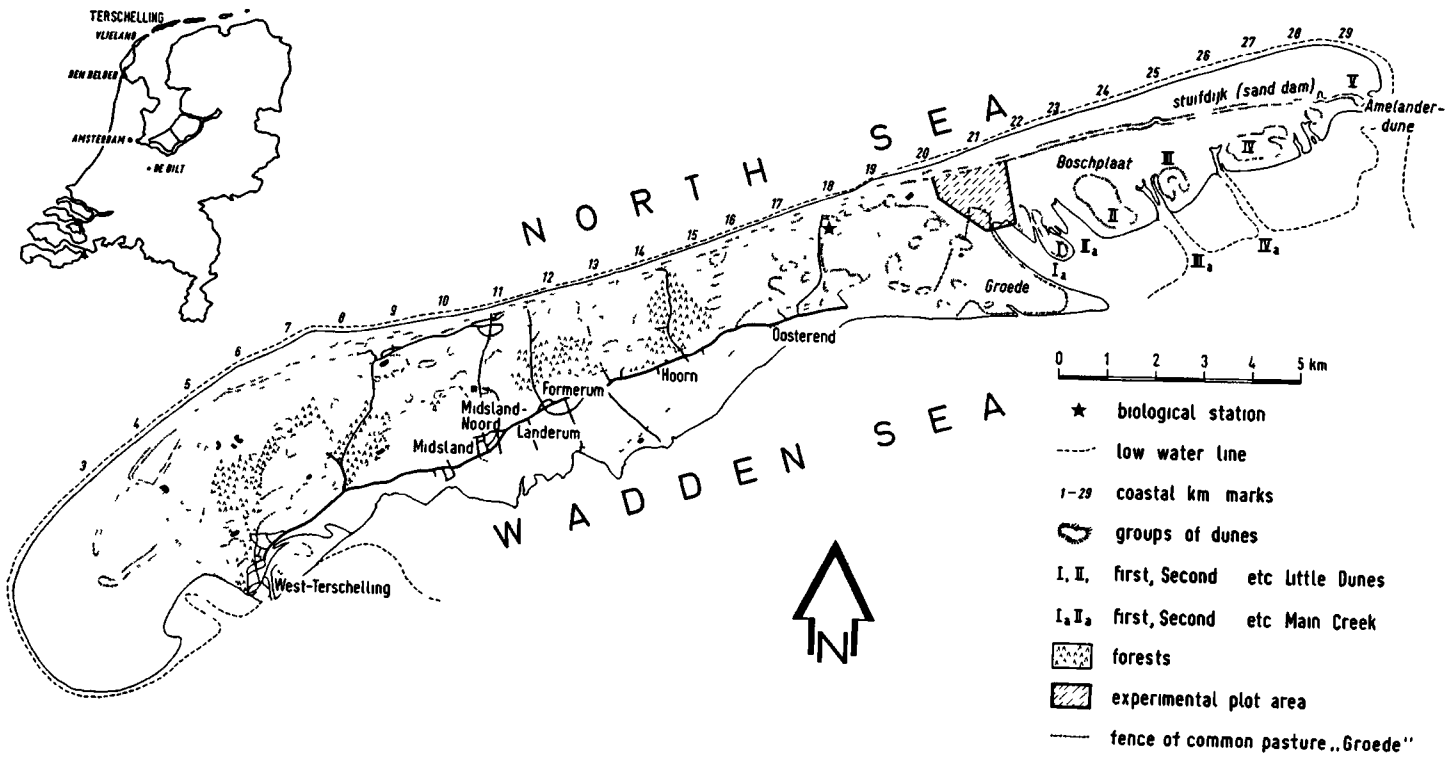

Fig.1. Map of the island of Terschelling

changes in soil structure took place and the gradual establishment of halophytes occurred. Westhoff (1947) studied this development from 1937 to 1946.

In the seres of halophyte associations which have existed since the forming of the Stuifdijk, distinction must be made between a silt halosere, in which succession occurs as a consequence of silt deposition and gradual de-salting, and a sand halosere in which the vegetation develops upon slightly silt-holding sand and in which de-salting, by means of precipitation and drainage water from the dunes is accompanied by irregularly occurring flooding so that a very changing salt content is present (Westhoff, 1947). These salt-marsh vegetations are regularly flooded by water from the Wadden Sea, via the sometimes deeply eroded creeks ('slenken') which lie between the 'Little Dunes'.

The most south-westerly part of the Boschplaat situated west of the former Koggediep, differs from the rest of the area by being much older – the former south-east point of the island – and by being used as pasture land. Even before the construction of the Stuifdijk it was the common pasture for cattle owned by the farmers from East Terschelling. This area is known as 'de Groede'. On the eastern side it is adjacent to the First Main Creek, and on the southern side to the Wadden Sea. The western side is adjacent to an area of dunes covered with dune heath, and the northern side to a varied salt-marsh area.

The grazed area consists of a few higher dune complexes surrounded by lower parts, some of which may be flooded irregularly during the winter at high-tide. Vegetation types of the hygroseres, haloseres and xeroseres occur with all their intermediate forms (Westhoff, 1947). In the course of the years the fenced boundaries of the area have been altered a few times, especially in the northern part. The pasture land is now 300 ha and is surrounded by a fence of ± 8 km long.

Besides Westhoff (1947, 1951: Westhoff & Brouwer, 1951) many other investigators have carried out botanical research on the Boschplaat, such as Van Dieren (1934); Van Dilst (1959); De Fouw (1962, 1963); Spekman & Groten (1963); Freysen & Van Heusden (1965); Freysen (1967a, 1967b); and Sterk (1968).

In the spring of 1966 an area of ± 150 ha, situated between km marks 20 and 22, was chosen for production research, as much as for practical reasons as for the fact that both grazed and ungrazed salt-marsh vegetations were present there. Moreover this area, as far as vegetation development is concerned, was the oldest (see above and fig.1).

Before production studies were carried out a detailed vegetation map (scale 1 : 2500) was made of this area (schematically shown in fig.2). For this purpose an aerial photograph taken in 1959, obtained from the Topographical Service in Delft, was used as a basis. In October 1970 several altitude measure-

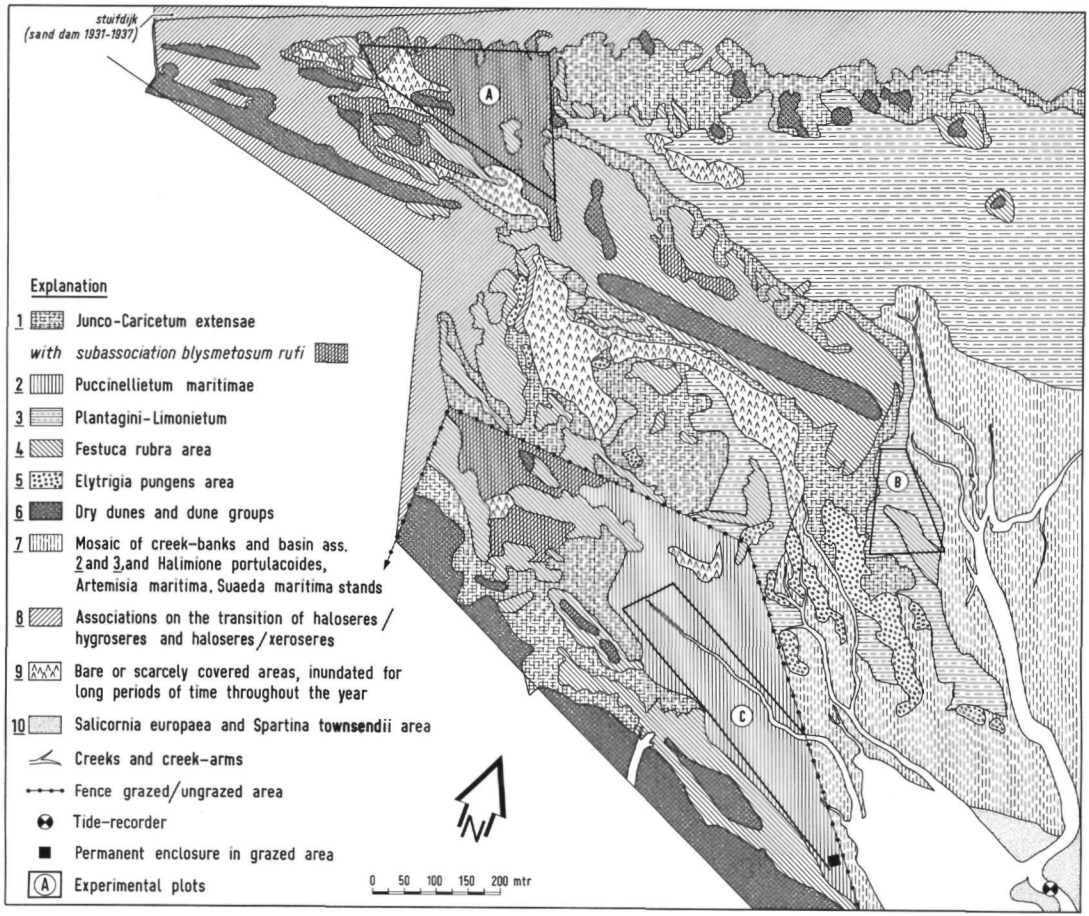

Fig.2. Vegetation map of part of the Boschplaat on Terschelling, between coastal km marks 20 and 22 in diagrammatic form. Surveyed from July to October 1966. See also fig.3.

ments were made. After the vegetation map had been made, three vegetation types were chosen from the halosere for detailed research. To a certain extent, these three types were representative of the whole area, and they were present in sufficient quantities to guarantee reliable results over the intended period of investigations. These are *Junco-Caricetum extensae* subass. *blysmetosum rufi* of the sand halosere, and *Plantagini-Limonietum* and *Puccinellietum maritimae* of the silt halosere. The latter site is grazed, the other two are not.

The experimental plots

According to Beeftink (1965) and Westhoff & Den Held (1969), the syn-systematic position of the three vegetation types is as follows:

Class:	Asteretea tripolii, Westhoff et Beeftink, 1962
Order:	Glauco-Puccinellietalia, Beeftink et Westhoff, 1962
Alliance 1:	Puccinellion maritimae, Christiansen, 1927 em.R.Tx., 1937
Association:	*Plantagini-Limonietum*, Westhoff et Segal, 1961
Association:	*Puccinellietum maritimae* (Warming, 1890), Christiansen, 1927
Alliance 2:	Armerion maritimae, Br.-Bl. et De Leeuw, 1936
Association:	*Junco-Caricetum extensae*, Br.-Bl. et De Leeuw, 1936 subass. *blysmetosum rufi*, Meltzer apud Westhoff, 1947; em. Westhoff et Beeftink, 1962.

The position of the three experimental plots is given in fig.2.

JUNCO-CARICETUM EXTENSAE SUBASS. BLYSMETOSUM RUFI (JC)

Junco-Caricetum extensae occurs on wet sandy plains which on the whole contain some silt and are only occasionally flooded, as a consequence of partial isolation from the sea by dunes or embankments; it also occurs at the foot of dunes bordering on salt-marshes where sufficient fresh water is present. The subassociation with *Scirpus* (Blysmus) *rufus* is limited in the Netherlands to the Wadden Islands. It is found in brackish dune slacks which are rarely flooded, or in depressions where rain-water stagnates.

The experimental plot is situated in the north-western corner of the Boschplaat furthest from the Slenk. In this infrequently flooded area the present vegetation developed in the ecotone between a salty and a fresh environment. Surrounded to a large extent by both the sand dikes (Stuifdijken) a gradual de-salting of this area is taking place. There is a great deal of sand-drifting from the 'new' Stuifdijk, especially in autumn and winter. The experimental plot is not a closed area with all the same vegetation. Several high and low *Festuca*

TABLE 1

Some vegetation records of the associations:

Junco-Caricetum extensae subass. *blysmetosum rufi, Plantagini-Limonietum* and *Puccinellietum maritimae*

Site	Junco-Caricetum extensae subass. blysmetosum rufi				Site	Plantagini-Limonietum				Site	Puccinellietum maritimae			
No. of record	1	2	1a	2a	No. of record	1	2	1a	2a	No. of record	1	2	1a	2a
Date	5/9'66	8/9'66	24/9'71	24/9'71	Date	17/8'66	17/8'66	24/9'71	24/9'71	Date	23/9'66	23/9'66	27/9'71	27/9'71
Surface area in m^2	5×5	5×5	5×5	3×3	Surface area in m^2	5×5	5×5	5×5	5×5	Surface area in m^2	7×7	3×3	2×2	2×2
Average height of veg. in cm	20	20	15	30	Average height of veg. in cm	17	20	12	12	Average height of veg. in cm	5	5	7	10
Coverage in %	60	50	95	95	Coverage in %	70	75	95	95	Coverage in %	75	85	65	85
Coverage of mosses in %			<1%											
Juncus gerardii	2.2	2.2	2.2	3.3	Plantago maritima	3 4	3 3	5 4	5.5	Puccinellia maritima	3.3	4 3	2.3	3.3
Plantago maritima	1.2	1.2	4.3	3.2	Limonium vulgare	2 2	2 2	2 3	3 3	Plantago maritima	3.3	2.2	2.3	2.3
Triglochin maritima	+.1	+.1	1.2	1.2	Triglochin maritima	2 1	1.2	1.1	1.2	Salicornia europaea	2.1	1.1	2 1	2.1
Scirpus rufus	2.2	2.3		+.1	Aster tripolium	1 2	1 2	1.1	1 1	Triglochin maritima	2.2	1.2	1.1	1.2
Carex extensa	2.2	1.2	2.2	(+)	Festuca rubra f litoralis	1 2	1.2	2 3	1.3	Spergularia media	1.1	1.1	1 1	1 2
Limonium vulgare	+.1		+ 1	+.1	Carex extensa	1 2	2 2			Suaeda maritima	+ 1	+.1	1.1	1.1
Agrostis stolonifera var. compacta subvar. salina	1.2	1.2	2.2	3.3	Juncus gerardii	1 1	+.1	1.1	+ 1	Aster tripolium	1.2	1.2	1.1	1.1
					Puccinellia maritima	+.1		+ 2	+.1	Limonium vulgare	1.2	+.2	1 2	1 2
Festuca rubra f litoralis	+.2		+.2		Armeria maritima		+.2	+.2	+.1	Glaux maritima	+.1	+ 1	1 1	1.2
Centaurium pulchellum	1.1		1.1	+.1	Glaux maritima	+ 1	+.1	+.1	+ 1	Spartina townsendii		+.2		1.2
Odontites verna ssp. serotina	+.1		1.1	1.1	Spergularia media	+.1	+.1	+.1	+.1	Cochlearia anglica	1.1	+.1		
Parapholis strigosa			+.1		Salicornia europaea	+.1	+.1	1 1	1.1	Halimione portulacoides	+.2			
Glaux maritima	1.1	1.1	1.2	1.1	Suaeda maritima		+.1	1.1	1 1	Juncus gerardii	1 1			
Aster tripolium	2.1	+.1	+.1	1.1	Cochlearia anglica	1.1	+.1	+.1		Armeria maritima				(+)
Salicornia europaea			r 1	(+)	Halimione portulacoides	+.1	+.1	+.1	+.1					
Artemisia maritima				(+)	Atriplex hastata			+.1						
Atriplex hastata			+.1	+ 1	Artemisia maritima			r 1						
Juncus alpino-articulatus ssp. atricapillus	+.1				Spartina townsendii		+.1							
Potentilla anserina		r.1	+.1	+.1										
Moss			+.2											

NOTE:
The taxa have not been arranged according to their presence as usual in record-tables, but according to their biomass as given in the tables of Chapter IV.

rubra clumps are present, as are low small dunes with *Hippophaë rhamnoides* shrubs. Zones with *Schoenus nigricans* extend along the sides of both dikes.

East of this area, and divided from it by several dunes and deep pools, lies an extensive sandy plain with a mixed vegetation of e.g. *Plantago maritima, Limonium vulgare, Puccinellia maritima, Triglochin maritima.* At high-tides the water from this side reaches the JC site; at very high-tides this can also occur via the gap in the old dam.

The altitude of JC varies from 119-127 cm + N.A.P. (average 122 cm + N.A.P.). (N.A.P. = New Amsterdam Level, Dutch Ordnance Date). Table 1 gives vegetation records from the area. The records of 1971 were taken from about the same place as those of 1966. In order to obtain these records, the Braun-Blanquet method (Braun-Blanquet, 1928, 1964) was applied.

PLANTAGINI-LIMONIETUM (PL)

This association, provided there is no grazing, develops on high sandy flats with silt deposits, on silt-rich areas at the foot of low dunes and embankments, and on the transition between basin and creek banks. In the Netherlands, this association is mainly found on the Wadden islands, because there relatively more ungrazed salt-marshes are present than in the south-westerly estuary area. On the Boschplaat, where a lot of silt is deposited on the former sandy flat, the association covers large areas (Westhoff & Segal, 1961). The experimental plot is situated at the end of the old Stuifdijk in a creek bank and basin area between the creek-arms of the First Slenk. With the exception of the north-west side, and depending on the silt content of the soil and the salinity of the soil moisture, PL joins a mosaic of vegetation types from creek baks and basins, such as *Halimionetum portulacoidis, Artemisietum maritimae* and *Atripliceto-Elytrigietum pungentis* (cf. Beeftink, 1965). In the north-west more highly situated *Festuca rubra* vegetations are to be found at the foot of the dam. A small belt of *Carex extensa* and *Juncus gerardii* is often present at the border of the adjacent dunes.

PL is situated at an altitude of 109-116 cm + N.A.P. (average 113 cm + N.A.P.) and is submerged a few times almost every month. Table 1 gives a few vegetation records from 1966 and 1971.

This vegetation type is physiographically similar to *Plantagini-Limonietum*. The difference is of a biotic nature, the latter changing, under the influence of grazing, into a *Puccinellietum*. *Puccinellietum* occurs on low parts of the salt-marsh, particularly in basins between creek banks and creeks. In the Netherlands this vegetation type occurs very frequently in the Wadden area and in the estuary area of south-west Netherlands. In the last mentioned district *Puccinellietum maritimae* and *Plantagini-Limonietum* intermingle as a consequence of grazing.

PM is situated in the north-east corner of the grazed part of the Boschplaat, running parallel to the easterly fence. Outside this fence vegetation types exist which correspond with PL and its surroundings. PM is adjacent to a row of dunes on its westerly side. The altitude of the study site varies from 106-116 cm + N.A.P. (average 112 cm + N.A.P.). Although the average altitude is scarcely lower than PL, the area is more frequently flooded, especially the low-lying parts. The site is situated closer to the creek, and moreover the creek-arm, which runs through the area, has hardly any shore banks. Vegetation records from this experimental plot are given in table 1.

Soil conditions

In August 1968 the area where the experimental plots are situated was surveyed by the Rijksdienst voor de IJsselmeerpolders (Government Department for the IJsselmeerpolders). Samples were taken from 1-3 points per ha depending on the soil conditions. It was only necessary to take samples up to a maximum depth of 50 cm. The previously mentioned vegetation map of this area was used as a basis for the soil survey. The results are shown in fig.3. JC is situated upon the border of an area with clay deficient sand that is found in the north (next to the Stuifdijk) and in the west, and of an area where a thin layer (0-5 cm) of sandy clay is deposited on this clay deficient sand. The borders between these areas are not very sharp. The clay deficient sand areas are situated somewhat higher and are not often flooded. As a result of plant growth a layer of organic material, humus, has gradually developed. The humus layer is 5-6 cm thick on the lowest parts (where JC also occurs) and the transition into sand is quite abrupt. On the higher parts, at the foot of both the sand dikes, the humus layer is thicker 10-12 cm, and the transition into sand is more gradual. The same humus top layer of the easterly and largest part of JC contains a little more silt. The organic material consists mainly of semi-decayed root remains.

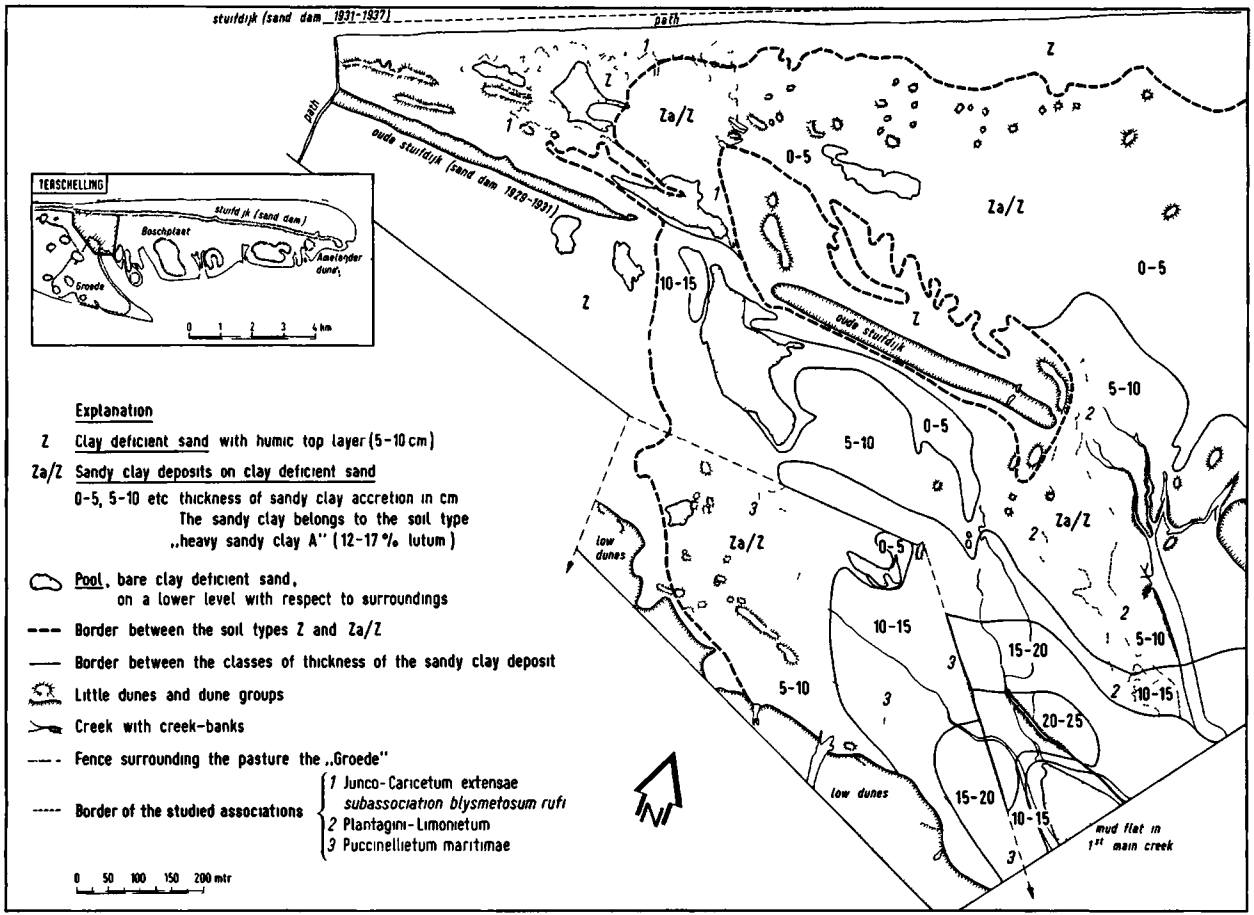

Fig 3. Soil conditions of part of the Boschplaat on Terschelling between coastal km marks 20 and 22. Surveyed by the Government Department for the IJsselmeerpolders in August 1968 See also fig. 2.

The sand of the Boschplaat is considered as belonging to the soil type clay deficient, moderately fine sand A, that is to say the size of the sand particles is 140-205 μ and the lutum content (clay content) 0-1.5% (lutum = particles $< 2\ \mu$). The sandy clay deposits belong to the soil type heavy sandy clay A, that is to say the lutum content is 12%-17% (Glopper, 1967). Sandy clay deposits are silt deposits in which the lutum content varies from between 5% and 25%. Readers are referred to Crommelin (1940), Favejee (1951), Van Straaten (1954, 1959) and Veenstra (1971) for the origin of the deposits in the Wadden area.

The extensive area adjacent to JC and north of the old Stuifdijk and the creek arms, is generally situated somewhat lower than JC. The basis of the deposits on this former North Sea beach lies between 100-105 cm + N.A.P. (Hollmann, 1962). The sandy clay layer is only 2 cm thick in the centre. From north (Stuifdijk) to south (Wadden Sea) the thickness of the sandy clay layer increases to 25 cm. The experimental plots PL and PM are situated in this silt-rich area. The thickness of the sandy clay layer in PL varies from 5-10 cm, in PM from 15-20 cm. The difference in thickness is presumably due to the difference in age of the deposits. Even before the construction of the dike, silting up occurred east of the Groede dunes. The basis of these mud deposits lies ± 85 cm + N.A.P. (Hollmann, 1962).

The sharp and therefore very noticeable difference in thickness of the deposits in PM and the immediately adjacent area outside the fence (see fig.3), must be explained by the difference in plant coverage of the sites. In PM an open vegetation covering is present due to grazing, while in winter the area is, to a large extent, bare. Less silt particles can attach themselves to the plants than in the densely grown, ungrazed adjacent vegetations (cf. Chapman, 1960; Hollmann, 1962). There is also a great deal of erosion due to grazing (trampling).

The top layer of the soil profile in PL and PM also contains an amount of organic material, consisting mainly of non-decayed or semi-decayed root remains. The amount of material varies depending on the nature and density of the plant growth and on its age.

The sandy clay deposits generally have a high water content and are to a large extent aerated. In the south, however, where the layer is thicker, the underneath part of the deposit is often non-aerated. This soil is lower lying and consequently is more often submerged.

The pools in the charted area are usually bare, or have a very limited plant coverage. In periods when there is no rain or flooding (May-June) they become temporarily dry. The soil consists of clay deficient sand with a muddy layer. In the creek in the south-eastern part of the surveyed area a sand flat runs dry at low-tide. The soil of this flat consists of clay-rich silt with a clay holding sand

underneath (3%-8% lutum).

The dunes are free from silt since they are only occasionally flooded. The banks along the creek arms predominantly consist of sand occasionally alternating with some silt layers. The creek banks are seldom broader than 1 m and the height amounts only to a few decimeters.

The general climate of the island of Terschelling

On account of its proximity to the sea and the influence of the Gulfstream the climate in the Netherlands is known as 'atlantic'. The relatively fairly cool summers and mild winters are characteristic. The prevailing west and south-west winds bring with them a great deal of rain during the whole year (Mörzer Bruyns & Westhoff, 1951).

The climate of the Wadden area can almost be called 'eu-atlantic', especially as far as temperature, humidity and wind are concerned. This does not completely apply to sunshine, evaporation and frequency of mist (see Westhoff, 1947). The winters are milder and shorter, the summers longer and cooler than in the middle and east of the Netherlands. Only in the south-west Netherlands, on the Zealand and Flemish coasts, and along the coast of the provinces of Holland, the winters are milder and the summers warmer (see also Barkman, 1959).

The following climatological data concerning the Wadden district are taken from Westhoff (1947) and Barkman (1959) and give an indication of the most important climatic factors of the Wadden district as a whole. Comparisons are made with inland, which in this case is understood by De Bilt, the main reference point of the inland climate of the Netherlands. See also Braak (1950), Mörzer Bruyns & Westhoff (1951) and Westhoff et al. (1970).

TEMPERATURE

The annual amplitude of the temperature is 13.7°C. Spring is usually 2-3 weeks later than inland. The temperatures are lower in spring and higher in autumn than inland. The close proximity of the sea delays the rise in temperature. The warmest month is August (16.4°C) and not July as is the case inland. The average daily maximum temperature in July is 18°C-20.5°C and in January 3.5°C-4.5°C; the average daily minimum temperature in July is > 14°C, in January > 0.5°C. Both the average daily temperature and the seasonal temperature variations are smaller than those of the inland area. There are less than 5 summer days (temperature > 25°C). The number of frosty days, 43 (min. temp. < 0°C) and the number of icy days, 8-10 (max.temp. < 0°C) is smaller than inland. The period in which these fall is shorter.

PRECIPITATION

The precipitation in May-June-July reaches 120-160 mm. The minimum amount of rain falls in April-May; inland in February; the maximum precipitation is in October; inland this is in August. In the period September-October-November precipitation reaches 200-240 mm. During the growing season there is 11% less precipitation than inland; in spring 15% less. There are large annual differences in the amount of precipitation. The average of ± 689-731 mm (Terschelling average 722 mm) is probably a little lower than inland. The rain mainly falls at night and in the early morning (4-8 h) with a minimum between 12-16 h. Compared with this most rain falls in the afternoon inland. Thunderstorms occur mainly in winter; inland mainly in summer.

RELATIVE HUMIDITY

The R.H. per 24 hours is higher from February to July, and in the other months lower than inland. The annual average is 83.1%. The R.H. at 14 h averages 42%-52% in June and July. The average, daily minimum R.H. is 46%-52%.

Considered over 24 hours, there is more evaporation than inland, especially in autumn and winter (stronger winds and more sun). In spring, however, there is less evaporation during the day.

WIND

The average wind velocity is 5.5-7.0 m/sec; this is almost twice as much as inland. There are more than 30 days per year with a wind velocity > 14 m/sec. The number of storm-force winds (> 7 Beaufort) is 30 times as many as inland. In winter there are three times as many stormy days than in summer.

In winter and autumn the S.W. wind is predominant. In summer it is usually the N.W. wind and in spring the N.E.

SUNSHINE

The number of hours of sunshine is higher than inland, especially in the growing period; from October to March it is a few hours less. The sun shines mainly in the afternoon. Both the number of clear days (cloudiness < 2) and the number of dull days (cloudiness > 8) are greater. The Wadden district has a relatively clear afternoon sky, especially in spring.

Mist occurs frequently in spring (20% of the annual total) and in winter (50% of the annual total); as far as inland is concerned these figures reach 10%-15% and 40% respectively. There is generally rather less mist than inland. Mist at 14 h is not infrequent.

DETERMINATION OF SOME ABIOTIC FACTORS AT THE TIME OF THE RESEARCH

Meteorological data

Until 1947 only a few systematic meteorological observations were carried out on Terschelling. Data about the weather were usually taken from the observation station Den Helder in the province of North-Holland (see fig.1), as did Westhoff (1947). An observation station was set up in 1947 for the measurement of precipitation and temperature by the Royal Netherlands Meteorological Institute (K.N.M.I. in De Bilt), at Hoorn-Terschelling, while in West-Terschelling the number of hours of sunshine (using a Campbell-Stokes heliograph), wind direction and velocity (10 m above ground level) are registered.

Combined meteorological data compiled between 1967-1971 in Hoorn-Terschelling (7 km from the IBP experimental plots) and West-Terschelling (17 km from the experimental plots), were used for the IBP research. For a few months (December 1966 to April 1967) corresponding data were collected near the Biological Station in Oosterend (3 km from the experimental plots, see fig.1). After comparing these observations with those of Hoorn and West, there appeared to be so little difference between them that the last mentioned observations were considered to be adequate.

The average daily temperature is given in table 2, the minimum and maximum temperatures, relative humidity (R.H.) and precipitation are also stated. The trend of a few of these parameters is shown graphically in figs.4 and 5.

Table 3 and 4 give wind direction and velocity respectively, while table 5 gives the number of hours of sunshine and cloudiness during the years in which the research was carried out.

According to the K.N.M.I., the weather in the Netherlands in 1967 was on the warm, wet and dull side; in 1968 it was mainly cold during the day and there was more than normal precipitation; there was also a shortage of sun. In 1969 there were very few deviations from the average temperature and precipitation; the weather was rather dull. In 1970 the weather was on the cold, wet and dull side.

TABLE 2

Average air temperature, average minimum and maximum temperatures, relative humidity (R.H.) and precipitation (per decade and per month) in the years from 1967 to 1970 inclusive on Terschelling

Year		1967					1968					1969					1970				
Month	de-cade	air temp. °C	max. temp. °C	min. temp. °C	R.H.	rain-fall mm	air temp. °C	max. temp. °C	min. temp °C	R.H.	rain-fall mm	air temp. °C	max. temp. °C	min. temp. °C	R.H.	rain-fall mm	air temp. °C	max. temp. °C	min. temp. °C	R.H.	rain-fall mm
January	I	1.5	3.4	−1.5	79	17.5	0.4	2.5	−2.7	83	25.3	1.9	3.3	0.4	95	3.1	−0.8	1.0	−3.9	91	14.6
	II	4.5	5.6	3.2	90	4.8	3.0	4.8	0.5	86	29.4	3.6	5.0	1.7	97	26.6	−0.7	0.8	−1.9	95	8.5
	III	5.1	6.3	3.4	92	40.3	4.8	6.1	3.1	89	8.3	5.7	7.1	3.8	96	17.5	−0.7	0.8	−2.3	94	11.1
per month		3.7	5.1	1.7	87	62.6	2.7	4.5	0.3	86	63.0	3.7	5.1	2.0	96	47.2	−0.7	0.9	−2.7	93	34.2
February	I	6.3	7.8	4.5	86	8.0	3.1	4.6	1.5	87	12.4	3.0	4.7	1.1	83	31.7	1.7	4.1	−1.6	88	22.8
	II	2.0	4.3	−0.4	82	12.7	2.5	4.5	0.1	85	1.2	−2.1	−0.1	−4.2	89	5.7	−0.4	2.1	−3.3	88	21.6
	III	6.2	8.1	4.2	79	25.6	1.0	2.8	−0.8	87	2.5	0.9	2.2	−0.6	94	10.8	2.7	5.0	0.8	89	33.1
per month		4.8	6.7	2.8	83	46.3	2.2	4.0	0.3	86	16.1	0.6	2.3	−1.2	88	48.2	1.3	3.7	−1.4	88	77.5
March	I	7.6	9.8	5.3	83	2.9	3.4	5.4	1.1	87	9.7	1.2	3.8	−1.8	86	0.0	1.5	3.6	−0.7	87	14.9
	II	6.8	8.5	4.6	79	9.4	5.1	7.2	3.0	79	18.4	−0.2	1.6	−1.8	88	45.6	3.5	5.3	1.2	89	5.0
	III	6.7	8.5	4.4	81	31.2	8.5	11.6	5.6	81	11.0	2.0	3.9	−0.4	85	5.6	3.3	5.5	1.2	90	22.0
per month		7.0	8.9	4.8	81	43.5	5.7	8.1	3.3	82	39.1	1.0	3.1	−1.3	86	51.2	2.8	4.8	0.6	89	41.9
April	I	6.4	8.1	3.4	79	23.5	4.9	7.1	1.2	74	14.3	7.0	10.9	2.5	82	10.8	2.9	4.7	0.0	83	17.7
	II	8.4	10.9	5.7	82	19.8	10.4	14.1	5.6	67	0.8	5.0	7.1	2.4	81	30.8	6.9	9.4	4.2	87	28.6
	III	7.5	9.9	3.4	73	10.1	11.9	15.0	6.3	83	14.5	8.4	11.0	5.0	87	13.3	7.7	9.3	5.3	83	30.2
per month		7.4	9.6	4.2	78	53.4	9.1	12.1	4.4	74	29.6	6.8	9.7	3.3	83	54.9	5.8	7.8	3.2	84	76.5
May	I	10.6	13.6	6.2	68	4.8	9.8	12.1	7.3	82	23.0	9.9	12.5	6.5	93	6.4	12.4	15.6	8.1	83	3.4
	II	13.5	16.5	9.5	80	38.0	9.2	10.9	5.8	78	45.2	11.6	14.4	8.3	89	43.7	11.8	14.0	8.6	81	0.6
	III	13.1	15.8	9.5	82	42.8	13.0	15.9	9.2	78	22.0	12.0	14.7	8.0	84	9.6	11.4	13.8	8.0	82	9.3
per month		12.4	15.3	8.4	77	85.6	10.7	12.9	7.4	79	90.2	11.2	13.9	7.6	88	59.7	11.9	14.5	8.2	82	13.3

June	I	13.1	15.5	10.4	79	1.3	14.5	16.5	11.0	80	9.4	12.2	14.2	8.9	81	19.1	16.7	19.4	11.7	69	0.3
	II	13.3	15.3	10.7	81	2.5	16.9	19.2	12.5	79	1.0	16.9	19.8	12.5	78	19.5	16.1	19.0	11.9	68	0.0
	III	15.9	18.1	12.7	80	12.3	15.6	17.8	11.8	82	45.0	16.0	18.1	12.5	83	6.8	17.9	20.9	12.6	72	18.0
per month		14.1	16.3	11.2	80	16.1	15.7	17.8	11.8	80	55.4	15.0	17.4	11.3	81	45.4	16.9	19.8	12.1	70	18.3
July	I	17.1	19.6	11.0	75	2.0	16.9	20.0	13.2	80	27.3	15.4	17.7	11.9	81	32.2	17.0	19.6	13.1	78	43.8
	II	18.6	21.3	14.8	79	3.8	15.4	18.0	12.2	77	49.7	18.1	20.6	13.5	78	4.4	14.7	17.1	11.5	79	32.3
	III	18.3	20.4	13.5	77	13.2	16.3	18.1	13.4	78	21.9	19.7	22.6	15.7	88	1.2	16.3	19.0	12.2	82	42.7
per month		18.0	20.4	13.1	77	19.0	16.2	18.7	12.9	78	98.9	17.7	20.3	13.7	82	37.8	16.0	18.6	12.3	80	118.8
August	I	18.7	21.4	13.6	78	15.1	18.5	20.5	16.1	83	5.6	21.5	24.7	16.5	77	7.3	18.5	20.7	15.3	82	7.2
	II	16.5	18.6	13.3	76	27.3	15.0	17.4	12.1	78	55.7	19.1	22.1	15.3	78	19.5	16.4	19.4	12.2	77	20.2
	III	17.2	19.5	13.8	83	0.0	17.8	19.9	15.4	88	11.1	15.3	17.6	12.7	84	93.7	16.5	19.3	10.9	84	1.7
per month		17.5	19.8	13.6	79	42.4	17.1	19.3	14.5	83	72.4	18.6	21.5	14.8	80	120.5	17.1	19.8	12.8	81	29.1
September	I	14.8	17.3	10.3	80	67.9	16.8	19.7	12.7	88	36.1	15.8	18.1	12.6	83	4.8	15.6	17.7	12.2	75	20.9
	II	15.2	17.3	12.3	88	17.5	14.7	17.2	12.2	86	68.1	17.6	20.7	14.0	82	7.9	14.5	17.2	11.5	85	74.3
	III	16.0	19.0	12.3	87	11.1	13.8	15.5	11.7	85	78.3	14.1	16.9	10.5	75	5.5	14.3	17.4	9.9	82	0.1
per month		15.3	17.9	11.6	85	96.5	15.1	17.5	12.2	86	182.5	15.8	18.6	12.4	80	18.2	14.8	17.4	11.2	81	95.3
October	I	13.8	15.7	11.0	80	27.8	13.7	15.3	11.5	93	45.7	14.1	17.1	10.0	91	12.9	12.2	14.8	9.0	84	26.1
	II	12.0	13.9	9.2	78	63.2	12.0	14.2	9.0	81	44.0	11.9	14.8	8.8	96	1.2	11.1	13.6	8.1	85	6.3
	III	10.6	12.4	8.0	83	42.0	11.2	13.4	8.5	91	5.5	12.4	14.1	10.2	86	24.1	10.9	12.7	8.7	84	36.7
per month		12.1	14.0	9.4	81	133.0	12.3	14.3	9.7	88	95.2	12.8	15.3	9.7	91	38.2	11.4	13.7	8.6	84	69.1
November	I	7.5	9.5	5.7	87	58.1	7.3	9.2	5.9	86	45.5	9.5	11.8	7.0	77	36.1	8.9	11.4	6.5	79	46.9
	II	7.7	10.0	5.0	84	10.9	3.5	4.9	1.4	88	6.9	7.7	9.6	5.4	86	34.8	7.3	9.3	5.2	89	51.9
	III	6.1	8.1	3.1	89	15.9	6.1	7.9	4.3	92	17.0	4.8	6.9	2.0	86	39.8	6.3	8.4	4.6	94	25.6
per month		7.1	9.2	4.6	87	84.9	5.6	7.3	3.9	89	69.4	7.3	9.4	4.8	83	110.7	7.5	9.7	5.4	87	124.4
December	I	5.3	7.3	3.0	81	24.7	0.5	1.9	−0.6	89	0.2	2.4	4.5	−0.4	93	28.0	7.9	9.3	5.8	85	21.5
	II	5.1	6.7	2.7	82	20.6	−1.5	0.1	−3.9	90	1.6	−2.0	−0.2	−4.0	96	7.8	6.0	7.8	4.1	89	2.2
	III	5.4	7.0	3.5	86	41.1	2.0	3.9	−1.3	86	35.0	−1.7	−0.1	−3.7	91	10.7	−0.2	2.1	−2.5	82	20.4
per month		5.3	7.0	3.1	83	86.4	0.3	2.0	−1.9	89	36.8	−0.4	1.4	−2.7	93	46.5	4.6	6.4	2.5	85	44.1
annual total		10.4	12.5	7.4	81.5	769.7	9.4	11.5	6.6	83.3	848.6	9.2	11.5	6.2	86	678.5	9.1	11.4	6.1	83.7	742.5
vegetation season		14.1	16.6	10.4	79.3	313.0	14.0	16.4	10.5	80.0	529.0	14.2	16.9	10.5	82.3	336.5	13.8	16.3	10.0	79.7	351.3

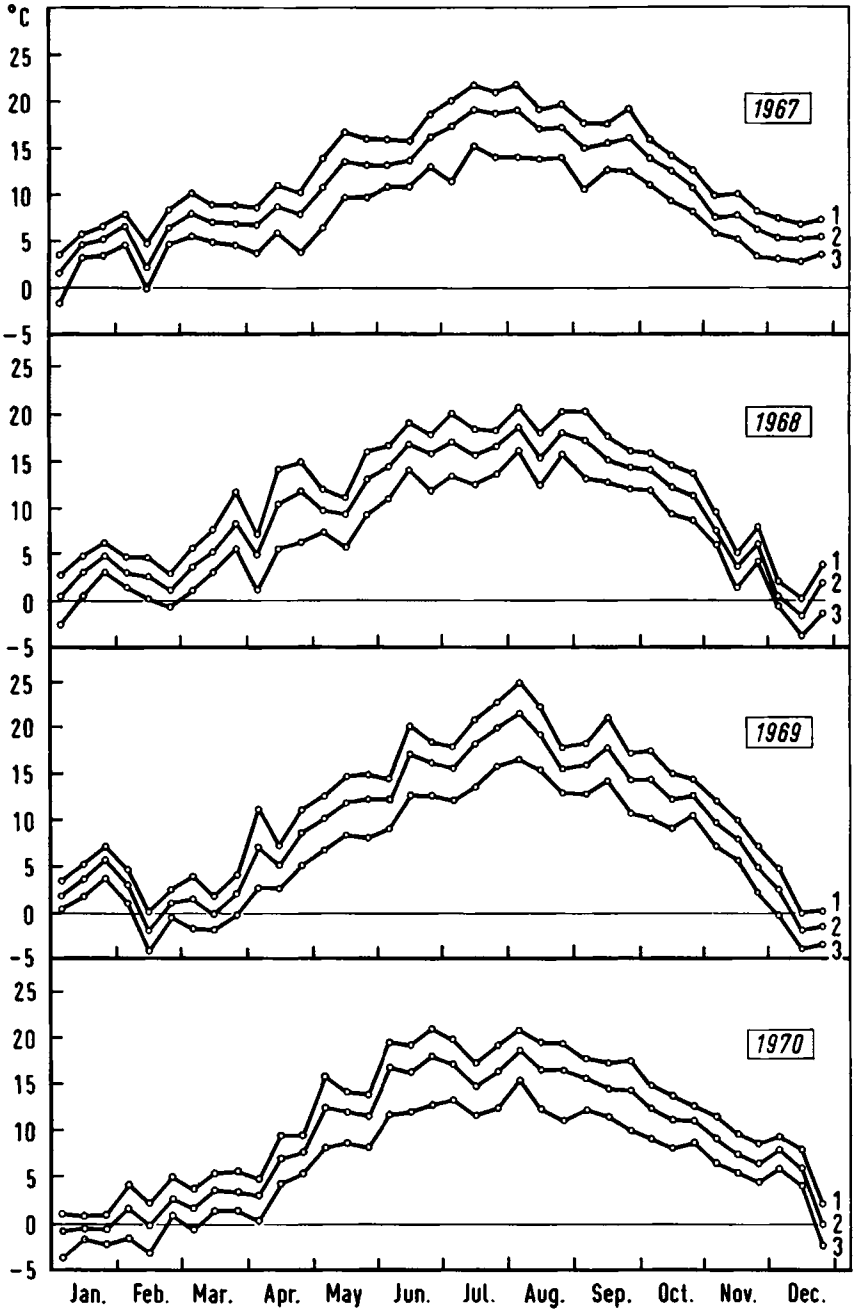

Fig.4. Air temperature curves for Terschelling from 1967 to 1970 inclusive. 1. decade means of maximum temperatures; 2. decade means of diurnal temperatures; 3. decade means of minimum temperatures

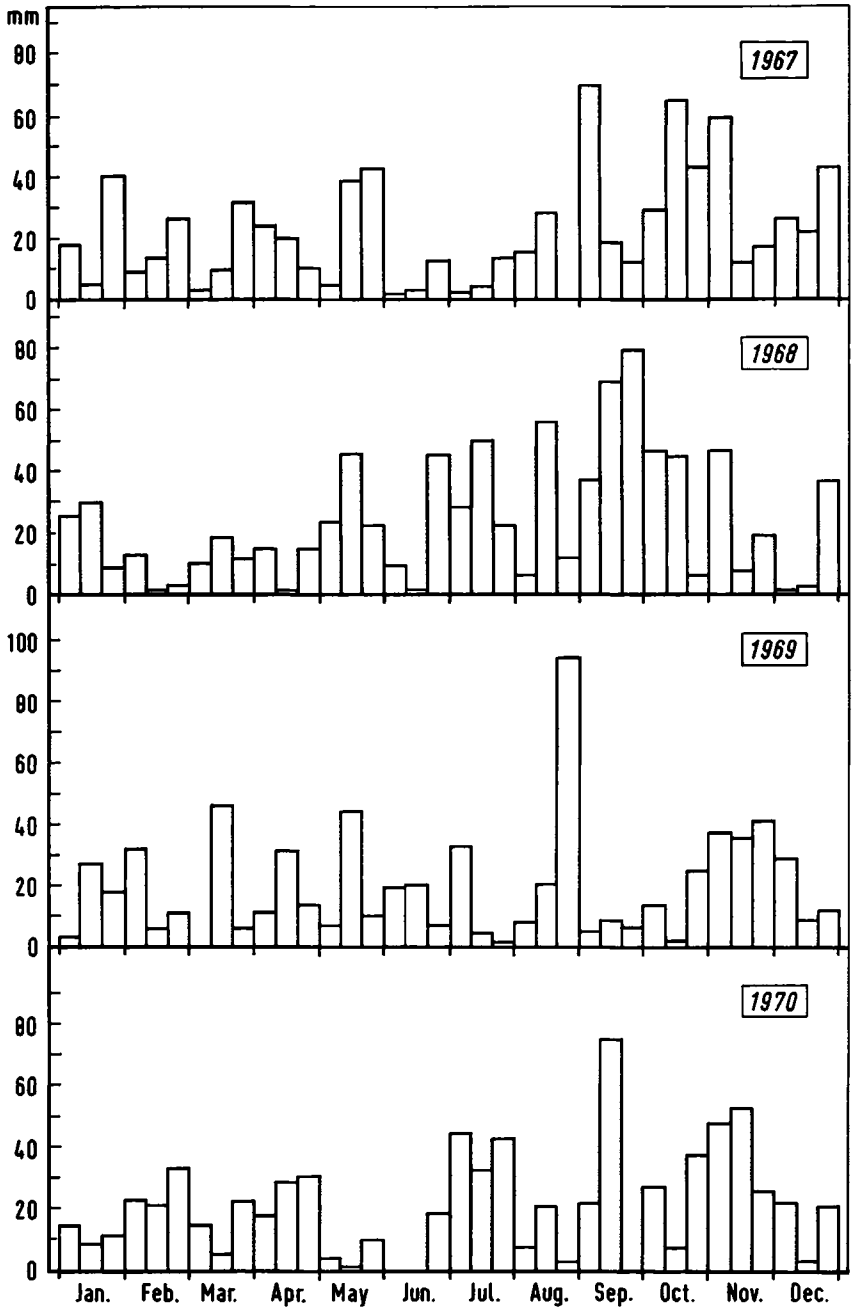

Fig.5. Precipitation curves for Terschelling from 1967 to 1970 inclusive. Values in mm per decade.

TABLE 3

Wind direction in the Wadden area from 1967 to 1970 inclusive.

The values are given in percentage frequency. The values of 1967, 1968 and January, February, May, June and December 1970 were derived from Station Vlieland (see fig.1), the others from West-Terschelling.

Wind direction			NNE	NE	ENE	E	ESE	SE	SSE	S	SSW	SW	WSW	W	WNW	NW	NNW	N
Code		00	02	04	06	08	10	12	14	16	18	20	22	24	26	28	30	32
January	1967	–	1	4	2	3	2	4	7	15	11	11	6	7	10	10	6	2
	1968	1	2	5	3	4	1	3	2	14	6	13	9	10	8	11	8	2
	1969	–	1	–	–	2	3	13	11	24	10	8	8	7	8	4	1	1
	1970	–	1	1	5	11	18	21	12	8	3	3	4	5	3	3	1	1
February	1967	–	2	1	1	9	6	8	3	6	6	10	16	12	9	4	4	3
	1968	1	5	13	14	12	5	6	2	8	3	6	5	7	3	3	2	4
	1969	–	8	7	5	23	10	5	3	6	4	3	3	4	3	7	5	7
	1970	–	3	8	6	4	1	4	5	5	4	7	8	16	12	7	5	6
March	1967	–	–	–	–	1	–	–	1	5	5	19	21	21	11	9	4	3
	1968	–	2	4	–	4	3	2	1	4	5	25	10	11	9	7	8	4
	1969	–	4	9	13	25	25	1	–	–	–	4	5	3	3	2	3	3
	1970	–	1	7	9	3	2	2	2	3	4	6	12	14	10	14	8	5
April	1967	–	6	12	9	9	1	2	1	2	3	8	8	8	6	9	8	7
	1968	1	7	10	7	9	4	7	4	4	3	10	8	9	2	4	5	8
	1969	–	2	7	5	7	3	5	3	4	3	8	11	6	9	11	9	8
	1970	–	4	3	3	4	3	2	1	1	4	13	15	8	5	11	17	8
May	1967	1	3	4	5	2	5	8	4	10	14	20	5	7	4	4	4	3
	1968	–	6	11	6	11	3	1	1	4	8	10	3	5	5	7	10	8
	1969	–	3	6	11	12	8	4	2	2	3	10	15	7	3	7	4	4
	1970	–	4	9	11	13	6	2	2	4	2	2	4	11	7	13	5	5

June	1967	–	11	5	3	1	1	–	1	1	9	17	4	7	11	3	11	17
	1968	–	9	11	8	4	1	2	2	5	8	21	11	4	2	2	4	6
	1969	–	13	20	6	6	3	2	2	2	5	5	5	7	6	8	5	4
	1970	–	4	8	16	16	2	2	1	1	3	8	5	8	6	4	9	9
July	1967	1	3	8	10	4	2	3	2	4	8	22	8	10	4	6	3	5
	1968	–	10	11	4	4	3	6	1	2	3	9	3	4	3	12	10	15
	1969	–	7	7	3	4	2	3	3	2	1	6	11	10	14	13	9	7
	1970	–	1	1	1	2	1	2	3	5	5	15	18	18	12	7	9	2
August	1967	2	2	7	5	6	4	3	2	7	5	14	16	11	5	2	4	5
	1968	–	13	20	10	8	1	1	1	5	5	5	5	7	6	5	2	6
	1969	–	5	4	6	11	9	4	2	1	1	3	5	3	6	13	13	14
	1970	–	7	10	15	11	1	3	7	5	5	5	9	5	5	6	5	3
September	1967	1	4	9	7	3	2	4	7	13	10	13	14	6	4	1	1	3
	1968	1	2	7	9	7	3	4	5	12	7	10	7	11	4	6	1	3
	1969	–	5	9	5	8	7	3	3	7	6	6	7	8	6	7	4	10
	1970	–	5	3	1	1	3	9	4	6	10	13	11	13	13	5	2	1
October	1967	–	–	–	–	–	2	1	2	13	22	23	15	13	5	2	1	1
	1968	1	–	1	2	5	3	4	4	16	8	11	14	19	5	3	1	2
	1969	–	1	2	3	6	8	7	7	6	9	9	4	9	11	14	3	–
	1970	–	–	1	2	5	9	7	5	4	8	8	12	11	9	9	7	6
November	1967	–	2	–	1	2	3	7	5	20	13	9	7	9	6	8	5	4
	1968	–	3	9	16	17	3	4	6	23	6	2	2	3	–	1	2	4
	1969	–	3	1	1	1	2	3	5	8	9	6	17	18	7	11	5	3
	1970	–	–	–	1	2	4	4	8	18	19	7	11	9	8	6	3	1
December	1967	–	3	3	–	–	–	1	1	3	7	11	12	15	10	16	13	5
	1968	–	2	2	6	30	11	8	7	10	2	1	–	2	2	4	5	9
	1969	–	2	1	3	15	12	7	18	16	7	4	1	1	2	2	2	5
	1970	–	5	4	4	10	6	3	1	5	10	9	7	5	7	8	8	8

TABLE 4

Average wind velocity, in m/sec, per decade and per month in the Wadden area from 1967 to 1970 inclusive.
The values of 1967, 1968 and January, February, May, June and December 1970
were derived from Station Vlieland (see fig.1), the others from West-Terschelling.

Year	1967				1968				1969				1970			
	Decade			monthly	Decade			monthly	Decade			monthly	Decade			monthly
	I	II	III	average	I	II	III	average	I	II	III	average	I	II	III	average
January	6.9	6.6	6.6	6.7	7.0	8.7	7.4	7.7	7.2	7.9	8.1	7.8	6.3	6.6	5.9	6.3
February	7.0	8.5	10.8	8.6	8.2	4.7	5.7	6.2	9.6	8.8	7.7	8.8	7.8	7.0	5.9	6.9
March	9.7	9.6	8.3	9.2	7.6	11.0	8.4	9.0	6.7	11.8	7.4	8.6	7.2	8.8	9.3	8.5
April	7.1	6.3	5.7	6.4	7.8	5.6	3.9	5.8	6.1	9.5	7.4	7.7	6.4	7.1	11.2	8.2
May	6.0	6.4	6.5	6.3	6.5	6.6	5.5	6.2	6.1	8.4	5.7	6.7	5.2	5.7	5.7	5.5
June	5.3	5.9	6.6	5.9	5.3	5.3	8.2	6.3	6.8	5.3	6.4	6.2	5.4	4.5	4.9	4.9
July	4.5	4.9	5.5	5.0	5.8	5.9	5.2	5.6	6.3	6.0	5.0	5.8	8.5	8.0	7.2	7.9
August	4.5	7.3	4.3	5.3	4.5	6.9	5.1	5.5	4.8	5.8	9.1	6.7	6.4	7.7	4.2	6.0
September	7.0	5.4	5.1	5.8	3.9	6.5	8.5	6.3	4.2	6.1	8.8	6.4	10.5	8.4	5.6	8.2
October	9.5	9.7	8.5	9.2	4.7	7.6	5.0	5.7	6.5	5.3	8.3	6.7	9.4	8.3	10.9	9.6
November	8.9	5.4	4.6	6.3	7.5	6.4	5.7	6.5	13.6	12.7	7.4	11.2	12.0	10.8	7.1	9.9
December	8.1	7.0	7.6	7.6	6.4	6.3	6.4	6.4	7.1	6.9	7.7	7.2	6.7	5.9	7.5	6.7

During the years in which the research was carried out, most rain fell in 1968 (848 mm, see table 2); 1969 was a dry year, only 678 mm rainfall, with a peak in August (120 mm). April and June were often drier months than May. In all these years the amount of precipitation in Terschelling was less than the national average.

As far as precipitation in the growing season is concerned (April-September inc.), the years 1967, 1969 and 1970 show the same trend (313, 336 and 351 mm of rain, resp.). In 1968 a great deal of rain fell in this period (529 mm). The winter of 1969-1970 was cold, as was the spring of 1969. The temperatures of April 1968 and the summer of 1969 were relatively high (maximum values in July and August 1969 were 20.4°C and 21.3°C resp.). In 1967 the highest average temperature was in July; in the other years it was in August. The total number of hours of sunshine was the highest in 1970 and the lowest in 1967 (see table 5). The same applies as far as the number of hours of sunshine during the growing season is concerned.

The meteorological data will be discussed further in the chapter dealing with the above-ground and under-ground production. Hours of sunshine and cloudiness will be considered with the efficiency calculations (Chapter VII).

In 1969 and 1970 a few micro-climatological observations were carried out concerning soil temperature at depths of 5, 10 and 25 cm, and the vegetation temperature. Soil thermometers with mercury reservoirs and loose minimum and maximum thermometers with liquid and mercury reservoirs respectively, were used for this purpose. The minimum and maximum thermometers were placed in the vegetation in such a way that they were not exposed to direct sunshine. The number of observations was too small and too incomplete to be dealt with in detail. Generally there was little difference in soil temperature at varying depths, only 0.1°C-1.5°C. The difference in soil temperature between the three vegetations was also small.

By hourly observations of temperature in PL and PM, the maximum temperature at 5 cm depth appeared to be reached 2-4 hours later than the maximum air temperature, and at 10 and 25 cm depth 7 hours later than the maximum air temperature. The maximum was usually reached earlier in PL than in PM. The top layer of PM is much more compact, contains less air and water and is therefore less conductive for temperature (see also Adriani, 1945). The curves showing the temperature variation in one day at different depths agreed with each other (see Lepoutre & Willems, 1969). The maximum temperature found in the vegetation (± 0.5 cm above ground level) differed strongly per vegetation. The highest values (± 35°C) were in June-July 1970 measured at a maximum air temperature of 28°C. In 1969 the maximum temperature in the vegetation was lower (26°C in JC; 26°C in PL; 28°C in PM; Lepoutre & Willems, 1969). The ecological significance of the micro-climate in the salt-

TABLE 5

Number of hours of sunshine, average cloudiness and solar radiation (in gcal/cm^2) per decade and per month from 1967 to 1970 inclusive on Terschelling

Year		1967		1968			1969			1970		
Month	decade	hours of sunshine	average cloud-iness	solar radiation in gcal/cm^2	hours of sunshine	average cloud-iness	solar radiation in gcal/cm^2	hours of sunshine	average cloud-iness	solar radiation in gcal/cm^2	hours of sunshine	average cloud-iness
January	I	24.6	6.5	(450)*	15.4	8.0	343	4.1	9.2	558	14.2	8.5
	II	8.6	8.4	(361)	9.1	8.3	363	4.3	9.3	360	4.7	9.6
	III	1.5	9.5	(574)	13.0	8.8	490	0.8	9.6	659	13.9	8.2
monthly total		34.7	8.2	1385	37.5	8.4	1196	9.2	9.4	1577	32.8	8.8
February	I	19.3	6.9	(940)	14.0	7.5	848	12.9	8.3	1033	27.8	6.3
	II	38.6	5.8	1251	25.8	7.9	878	18.9	8.2	1024	23.3	7.6
	III	21.4	7.6	1139	26.1	8.0	666	4.2	9.7	1178	22.3	6.5
monthly total		79.3	6.7	(3330)	65.9	7.8	2392	36.0	8.7	3235	73.4	6.8
March	I	32.0	7.2	1596	23.5	8.2	2304	54.2	6.5	2104	50.2	6.5
	II	37.0	7.4	2571	38.1	7.2	1473	15.9	8.6	1861	22.9	7.7
	III	48.5	7.5	3209	49.8	6.6	2832	52.1	5.6	2770	45.5	7.8
monthly total		117.5	7.4	7376	114.4	7.3	6609	122.2	6.8	6735	118.6	7.3
April	I	46.6	7.6	3282	55.4	6.6	4085	88.2	4.2	2909	47.9	6.7
	II	59.1	6.9	4363	81.1	6.4	3713	59.2	7.8	2922	39.3	8.0
	III	90.9	5.0	3881	66.4	6.0	3928	52.7	6.9	3499	46.4	7.6
monthly total		196.6	6.5	11526	202.9	6.3	11726	200.2	6.3	9330	133.6	7.4
May	I	81.8	6.8	3059	27.1	8.8	2971	27.8	8.7	4287	71.8	6.2
	II	62.4	7.5	4075	59.6	7.5	3808	51.2	8.7	5293	85.8	5.4
	III	64.2	7.5	5370	80.8	6.2	5113	74.3	7.6	4594	55.2	7.6
monthly total		208.4	7.3	12504	167.5	7.5	11892	153.3	8.3	14174	212.8	6.4

June	I	52.8	8.3	4345	59.2	8.1	5610	99.4	4.8	6495	134.4	2.1
	II	70.3	7.1	5626	83.6	5.0	5446	100.0	5.7	5336	95.8	4.2
	III	64.2	7.6	3828	51.5	7.1	4167	48.0	7.8	4921	74.6	7.1
monthly total		187.3	7.7	13799	194.3	6.7	15223	247.4	6.1	16752	304.8	4.5
July	I	89.3	5.9	4593	73.0	6.7	3834	39.6	8.1	4388	58.5	7.2
	II	77.8	6.0	4313	55.5	8.2	5083	81.7	5.7	3334	37.6	8.7
	III	64.4	7.4	4764	68.4	7.3	4279	58.4	8.1	4342	63.7	6.9
monthly total		231.5	6.5	13670	196.9	7.4	13196	179.7	7.3	12064	159.8	7.6
August	I	62.5	7.1	3112	37.3	8.8	4651	93.2	6.1	4214	77.2	5.5
	II	54.5	8.0	3101	42.9	8.1	3773	62.6	7.3	3816	62.8	7.2
	III	44.8	7.5	3875	75.8	6.0	3248	42.5	8.8	4050	79.8	6.3
monthly total		161.8	7.5	10088	155.9	7.6	11672	198.3	7.4	12080	219.8	6.3
September	I	46.8	7.8	2902	54.9	7.2	2825	41.4	7.0	2584	32.8	8.1
	II	31.7	8.6	1854	32.0	7.5	3026	63.9	5.2	2570	48.4	8.1
	III	43.3	7.1	1196	12.9	8.6	2533	38.7	7.3	2270	46.1	7.7
monthly total		121.8	7.8	5952	99.8	7.8	8384	144.0	6.5	7424	127.3	7.9
October	I	22.5	8.5	1056	8.2	9.1	1882	36.1	6.6	1685	38.2	8.0
	II	20.1	8.2	1450	30.8	7.1	1450	30.0	7.0	1587	36.2	6.9
	III	26.6	7.4	1315	20.3	7.5	1140	20.9	8.2	865	12.0	8.3
monthly total		69.2	8.0	3821	59.3	7.9	4472	87.0	7.3	4137	86.4	7.8
November	I	20.8	8.1	679	10.0	9.1	745	14.4	8.4	869	19.1	8.3
	II	22.3	7.3	643	21.1	7.1	548	6.2	8.4	662	18.8	8.9
	III	14.6	8.1	452	9.0	9.0	460	11.4	8.0	545	14.6	8.6
monthly total		57.7	7.8	1774	40.1	8.4	1753	32.0	8.3	2076	52.5	8.6
December	I	7.4	9.3	202	0.0	9.6	439	10.6	8.9	388	11.2	8.1
	II	17.3	7.4	577	24.1	6.0	300	10.0	8.5	344	7.5	8.9
	III	8.3	9.1	426	4.7	7.9	424	12.2	7.4	359	18.6	8.7
monthly total		33.0	8.6	1205	28.8	7.8	1163	32.8	8.2	1091	37.3	8.6
annual total		1496.6	7.5	(86430)	1363.3	7.6	89678	1442.1	7.6	90675	1559.1	7.3
vegetation season		1498.8	7.2	67539	1017.3	7.2	72093	1122.9	7.0	71824	1158.1	6.7

*) The values between brackets indicate estimated values; no recording took place.

marsh is probably small when compared with the extreme edaphic factors (Westhoff, 1947).

Edaphic data

CHEMICAL ANALYSES

Soil samples were collected from the experimental plots in 1969 for closer analysis. The samples were obtained using an agricultural borer ('gutsboor'). A mixed sample consisting of 20 sub-samples taken at random from every plot was prepared.

Two soil layers were assembled separately, namely the 0-5 cm layer and the 5-20 cm layer. The samples were analysed at the Bedrijfslaboratorium voor Grond- en Gewasonderzoek (Laboratory for Soil and Crop Testing) in Oosterbeek, according to the methods described by De Vries & Dechering (1960). The following analyses were carried out:

a. with reference to the granular composition:
   - fraction of rough sand $> 105\ \mu$
   - fraction of fine sand $16\text{-}105\ \mu$
   - fraction of soil particles $< 16\ \mu$

These are the fractions which are set apart for clay soils in general soil research (Kuipers, 1962).

b. with reference to the chemical composition:
   - $CaCO_3$ and organic material in weight percentages of stove-dry soil (105°C).
   - pH-KCl.
   - P-Al = amount of available phosphate in mg P_2O_5 per 100 g soil; determined by means of extraction with rather weak ammonium lactate acetic acid.
   - K-HCl = amount of potassium, expressed in mg K_2O per 100 g stove-dry soil, which is found in the soil solution on the clay-humus complex.
   - K-value, calculated from the potassium content; the clay content and the carbonic acid content.

A closer analysis of the fraction of soil particles $< 16\ \mu$ was not carried out in the granular composition analysis. It can be assumed that, in marine deposits, the clay (= lutum)-fraction is about 2/3 of the silt fraction (Beeftink, 1965), although Hollmann (1962) found a large deviation in this value for the Boschplaat. For a more detailed survey of the granular composition of the Wadden sand and salt-marsh deposits on the Boschplaat the reader is referred to Holl-

TABLE 6

Soil properties of three salt-marsh communities on Terschelling

Site	Junco-Caricetum extensae subass. blysmetosum rufi				Plantagini-Limonietum				Puccinellietum maritimae			
Date	5-5-1969		10-10-1969		5-5-1969		10-10-1969		5-5-1969		10-10-1969	
Depth in cm	0-5	5-20	0-5	5-20	0-5	5-20	0-5	5-20	0-5	5-20	0-5	5-20
Coarse sand >105 μ –%			82	96			6	92			26	63
Fine sand 16-105 μ –%			8	1			34	3			36	21
Particles <16 μ –%			6	2			36	3			24	12
pH – KCl	6.8	7.3	7.0	7.7	6.9	7.1	6.9	7.2	7.3	7.5	7.1	7.7
$CaCO_3$ –%	1.4	0.4	1.0	0.6	2.0	0.7	1.7	0.8	5.3	2.0	4.2	2.5
Org. material –%	7.0	0.3	2.8	0.5	15.7	1.1	22.6	0.9	12.2	2.7	9.7	2.0
P – Al	7	3	5	2	18	4	23	3	30	9	43	10
K – HCl	48	8	39	13	250	26	157	28	132	54	146	60
K-value			103				78				143	

mann (1962) and Freysen (1967b).

The results of the soil analyses are given in table 6. There is a clear difference in all the investigated qualities between the JC soil and that of PM and PL. The differences between PM and PL are less. Low percentages for the fractions fine sand and silt, and a high percentage of rough sand are to be found in the top layer of JC. This site was and still is only infrequently flooded; moreover, drifting sand is occasionally deposited here.

The differences in percentage of rough sand and soil particles $< 16\,\mu$ between PL and PM must be explained by the difference in the manner of accretion. In PL the main deposition consists of fine silt particles brought by the low current through the smallest branches of the creek-arms. The site is flooded slowly and the water runs slowly back again, so that the silt particles have time to be deposited. The speed of the flood-water current in PM (closer to the creek) is much greater; the water in the creeks flows quickly over the creek-banks, which are low here; consequently a great deal of sandy material is carried along. The heavier particles are deposited before the silt; moreover, some of the silt particles are carried away again by the outgoing water (cf. Beeftink, 1965).

In JC and PL hardly any silt is found in the deeper layers (JC 2%; PL 3%). It is, on the other hand, found in PM (12%); as the soil survey indicated, the silt deposits are thicker there.

The pH of the soil in all three areas is similar. The somewhat higher pH in PM could be due to the higher lime content. The somewhat lower pH in the 5-20 cm layer is related to the decrease in the humus content.

The carbonate content is the lowest in JC (1.4%) and the highest in PM (4.2%-5.3%). In general the $CaCO_3$ content increases with the increased percentage of soil particles $< 16\,\mu$. This increase shows no linear relationship as a result of the unequal distribution of Ca in the silt particles (Verhoeven, 1962; Veenstra, 1971). Though PL is relatively rich in silt, the $CaCO_3$ content of its soil is not the largest one. This may be explained further by decalcification due to decomposition of the abundant organic matter. In PM the higher lime content is partly due to the influence of often large numbers of seagulls which stay here especially in winter but also in summer. Most of the shell material is brought by the seagulls. The lime content in the 5-20 cm layer is small, except in PM where there is a lot of silt present in this layer.

Higher percentages of organic material are found in the top layer of the soil profile than in that of the 5-20 cm layer. The amount of organic material is the highest in PL, and the lowest in JC. The difference in the amount of organic material corresponds with the difference in production and decomposition of this material. This will be discussed in more detail in the following chapters. The organic material consists mainly of non-decayed, semi-decayed and already humified root remains. Only a small part comes from above-ground plant

remains which are retained by the silt. As a consequence of the grazing in PM, plant material is trampled into deeper layers. Therefore, there is a higher content of organic material in the 5-20 cm layer compared with the corresponding layer in JC and PL. This is also probably due to the fact that the site of PM has been covered by vegetation for a longer period of time.

As well as this organic material, originating from matter produced on the spot (autochtonous organic matter, cf. Beeftink, 1965), there is the allochtonous material. The latter consists partly of the more or less humified particles which, together with the silt, are carried along by the flood water, and take part in the sedimentation process (as a rule, the humus content increases with the increased lutum content; see Beeftink, 1965). Another part of allochtonous material is formed by algae, which cling to the plants during flooding or which are deposited. Algae deposits have chiefly been observed in PM in spring and autumn. Algae development on the spot can, however, also play a part in the formation of humus; in this case, therefore, the organic matter is autochtonous. If, in spring, the sites are submerged, a huge growth of algae can take place. This is particularly the case in JC where the algae develop in the stagnating water; in PM a great deal of algae growth was noticed on the soil surface. In dry period the algae die off and humify. The flood water, however, besides supplying material also carries away plant parts (see Chapter V).

The factors P-Al and K-HCl give an idea about the nutrients in the soil. The values obtained are parameters for the amount of phosphor and potassium which is present, even though this is not directly available for the plants. High P and K values are found in PL and PM compared with JC. When the P-Al and K-HCl values are compared with those for other natural environments or for agriculture, one is struck by the wealth of potassium; potassium values of 13-26 are considered to be sufficient in agriculture (Kuipers, 1962). The P-Al value is very low, especially in JC. P-Al values of 30-40 are considered to be sufficient in agriculture. The much greater amount of P in PM is due to fertilization by cattle in this area. Fertilization by birds in the winter also plays a part in the supply of P.

The nitrogen content could not be determined, because the samples were not processed in time. As the amount of N is closely correlated to the amount of organic material, the latter can be used as an indication of the nitrogen content. The amount of N available to the plants varies during the season due to fluctuations in fixation and leaching, or to decomposition of organic material. More N is to be expected in PM than in PL due to fertilization. JC probably has the lowest N value (little silt, little humus).

The magnesium content was also not measured. It is to be expected that enough magnesium is present for the plants; there is a lot of Mg in the silt in the form of $MgCO_3$. The salinity (NaCl content) is considered elsewhere.

The large amounts of $CaCO_3$, K, and probably also Mg and Na in the top layer are attributed to the regular flooding by sea-water. This water is rich in these materials; moreover many minerals are present in the deposited silt, especially in the clay fraction ($< 2\ \mu$). Many of these materials are absorbed by organic matter and silt during flooding.

P and N are found in very small amounts in sea-water. The vegetation is dependent upon the amount of organic matter for these elements. The still relatively high P value in PL and PM possibly indicates that there is an accumulation of P. The phosphoric acid, released in the soil by the decomposition of organic material, combines with the Ca and Mg ions. It does not dissolve easily, and consequently the chance of it being leached out is smaller. It is, however, not easily available to the plants due to the high pH (Kuipers, 1962).

The decrease in $CaCO_3$ and K in the 0-5 cm layer, and the increase in these materials in the 5-20 cm layer from spring to autumn, indicate that they are leached by rain-water during the growing season when there is little flooding. The great difference in the occurrence of organic material in spring and autumn (JC 0.7%-2.8% resp.; PL 15.7%-22.6% resp.) cannot be explained. The content of organic material probably varies a great deal from place to place, and 20 sub-samples are not enough in order to discover reliable differences. The difference in P runs parallel with the difference in organic material. The large increase in P in PM can partly be attributed to fertilization by cattle during the growing season.

FLOODING FREQUENCES

Using a self-registering tide-meter (Pressure recorder type G/531, Negretti-Zamba), which was placed at the beginning of a creek-arm, not far from the experimental plots PL and PM (see fig.2), the water levels of every tide have been measured since November 1968, to within an accuracy of 5 cm. After calibrating, all the measured levels were calculated in cms + N.A.P.. Flooding frequencies of each biotope could be determined using these data and those concerning the altitude of the various vegetations which were measured in October 1970. Moreover personal observations in the field concerning the date and the duration of flooding of certain areas were used.

Table 7 gives the flooding frequencies per month of the three experimental plots. The frequencies for the period from March to October inclusive are also given.

As a result of the larger variation in the altitude of PM (106-116 cm + N.A.P., average 112) compared with that of PL (109-116 cm + N.A.P., average 113 cm) the flooding frequencies of these vegetations differ somewhat. If PM is com-

TABLE 7

Flooding frequencies of three salt-marsh communities on Terschelling

Site	Puccinellietum maritimae			Plantagini-Limonietum			Junco-Caricetum extensae subass. blysmetosum rufi		
Height of site, cm + N.A.P.	105-110			110-115			119-126		
Minimum water level for flooding, cm + N.A.P.	105			110			150		
Year	1969	1970	1971	1969	1970	1971	1969	1970	1971
Flooding frequency:									
January	5	1	19	4	1	14	1	–	–
February	10	12	(6)	7	12	6	1	3	–
March	2	11	7	2	10	6	–	2	–
April	(6)	10	2	5	10	2	–	1	–
May	3	(2)	(2)	2	2	1	–	–	–
June	5	(2)	(–)	1	(1)	–	–	–	–
July	6	14/16	3	(4)	9	3	–	–	–
August	8	5	(9)	5	5	6	–	–	–
September	5	15	(2)	4	14	2	1	–	–
October	13	20	15	10	17	9	3	7	3
November	32	12		30	11		8	5	
December	(2)	13		2	10		–	–	
Annual total	97	116		76	102		14	18	
Vegetation season total	33	48/50	18	21	41	14	1	1	0

Values between brackets are minimum values; due to defective meter there was no complete registration.

The observations finished in November 1971.

pletely flooded, at water levels of 110-115 cm + N.A.P. or higher, PL will also be flooded. In 1969 the number of floodings was 76, in 1970 it reached 102. At water levels of 105-110 cm + N.A.P., however, part of PM is still flooded (i.e. both sides of the creek-arm and the area between creek-arm and the fences, see fig.2); this is not so with PL. The difference in the situation of PL and PM, in regard to the creek and creek-arms, also determines the difference in flooding frequencies. During the vegetation season PL and PM are flooded chiefly during the period of the spring-tides.

The JC experimental plot, lying between 119-127 cm + N.A.P., is not flooded by water levels in the creek of up to 125 cm + N.A.P., as would perhaps be expected. JC is situated far from the creek and there are several barriers

between the creek and this plot. There must, therefore, be an excess of water present before it can reach JC. From personal observations it was shown that JC was not flooded until the height of water in the creek exceeded 150 cm + N.A.P.. The flooding frequencies given in table 7 are calculated on this basis. It appears from table 7 that May and June are dry months as far as flooding is concerned, while September, October, November and February are wet months. JC is mainly flooded in the period October-March, with the highest frequency in November. There was no flooding of JC during the vegetation season, except for once in September 1969 and again in April 1970, when the flood just reached it.

As far as tide is concerned, it is worth mentioning that during high-water in summer, the level is lower at night than during the day, and that during high-tide in the months from October to March, the level is generally higher than in the period from April to September. The average high-water on the Boschplaat is ± 81 cm + N.A.P., the average low-water 106 cm – N.A.P.. The tide difference is, therefore, ± 187 cm. The average daily difference is 24 cm at high-tide and 2 cm at low-tide.

It was not possible to determine the duration of flooding of the biotopes from the registration on the tide-recorder. This is very dependent on the height of the flood above the surface and the drainage possibilities of each separate plot. In PM the water drains quickly away again in the direction of the creek-arm: some water, however, remains in the hollows which exist due to grazing (i.e. trampling). In PL where the water has to flow further via the extremities of the creeks, in order to reach the vegetation, a delay occurs with the incoming water as well as with the outgoing water in comparison with the increase and decrease respectively of the water in the creek (cf. Beeftink, 1965). During frequent successive floods PL can, therefore, remain wet for longer periods of time (days); ± 1-5 cm water remains. This was the case for example in August 1969; during the winter this can happen even more often. In JC the flood-water always stagnates. After a flood has reached JC, ± 5 cm water remains which eventually disappears by evaporation and into the soil.

The level of the ground-water (see below) gives an indication of the duration of flooding in the experimental plots.

RATE OF SEDIMENTATION

The rate of sedimentation is closely related to the duration and frequency of flooding. The sedimentation rate was not studied during this research. The results of work carried out by Hollmann (1962), however, give good information on this subject. The lower limit of sedimentation is determined by the

level of the average high-water line; on the Boschplaat this is ± 80 cm + N.A.P.. The upper limit is situated, according to Hollmann, between 130-135 cm + N.A.P.. The annual duration of flooding above this height is too small to make the further depositing of clay possible. Sedimentation is also dependent upon plant coverage. With an increased vegetation density there is an increase in the rate of sedimentation at the same N.A.P. height. Hollmann found that, in a *Puccinellia maritima* stand, between 101-105 cm + N.A.P., having a plant covering of 85%, maximum sedimentation took place. The rate of sedimentation amounted to an average maximum of 7 mm annually. Using the sum of the flood levels above the surface, Hollmann calculated that in a *Plantago maritima-Limonium vulgare* community at 110-115 cm + N.A.P. (i.e. similar to experimental plot PL) maximum sedimentation is between 3.9 and 5 mm per year. The rate of sedimentation in PM will be lower than in PL as a result of less dense growth, especially in winter when hardly any plant material is present. Similar sedimentation rates are quoted by Chapman (1960) from Richards (1934) and Nielsen (1935); 4.4-7.8 mm per year for a *Puccinellietum*, 3.4-4.2 mm per year for a *Plantago maritima* community.

GROUND-WATER LEVEL

For ± 1½ year (May 1969 to December 1970) the ground-water level was measured at least once a week in the three studied communities. Plastic tubes (8 cm diameter), which were pushed into the soil up to a depth of ± 70 cm were used for this purpose. The water levels, above and below the surface, were determined using a measuring staff. In PM the tube was placed in the high side of the plot, in JC in the low side, and in PL about in the middle. The ground-water levels measured in this way are shown in fig.6. The values are all relative and give an impression of the seasonal variations in the ground water. Apart from precipitation and evaporation the ground-water level in PL and PM is also strongly influenced by the ebb and flow of the water in the neighbouring creeks. There are daily water level fluctuations with a periodicity of that of the tidal variations. The size of the fluctuations differs, however, from place to place in the plot, depending upon the situation in regard to the creeks, level of the tide in these creeks and the structure of the soil.

During hourly observations at 8 different places in PL and PM on June 12th and September 3rd 1970, when there was no spring-tide and the weather was calm and dull, the water level per tube fluctuated between 1 and 10 cm. The difference in level between the tubes themselves amounted to 15-25 cm. In July 1970, during a spring-tide, a daily variation of 30 cm was observed in some tubes in PL. It is beyond the scope of this publication to go more deeply into

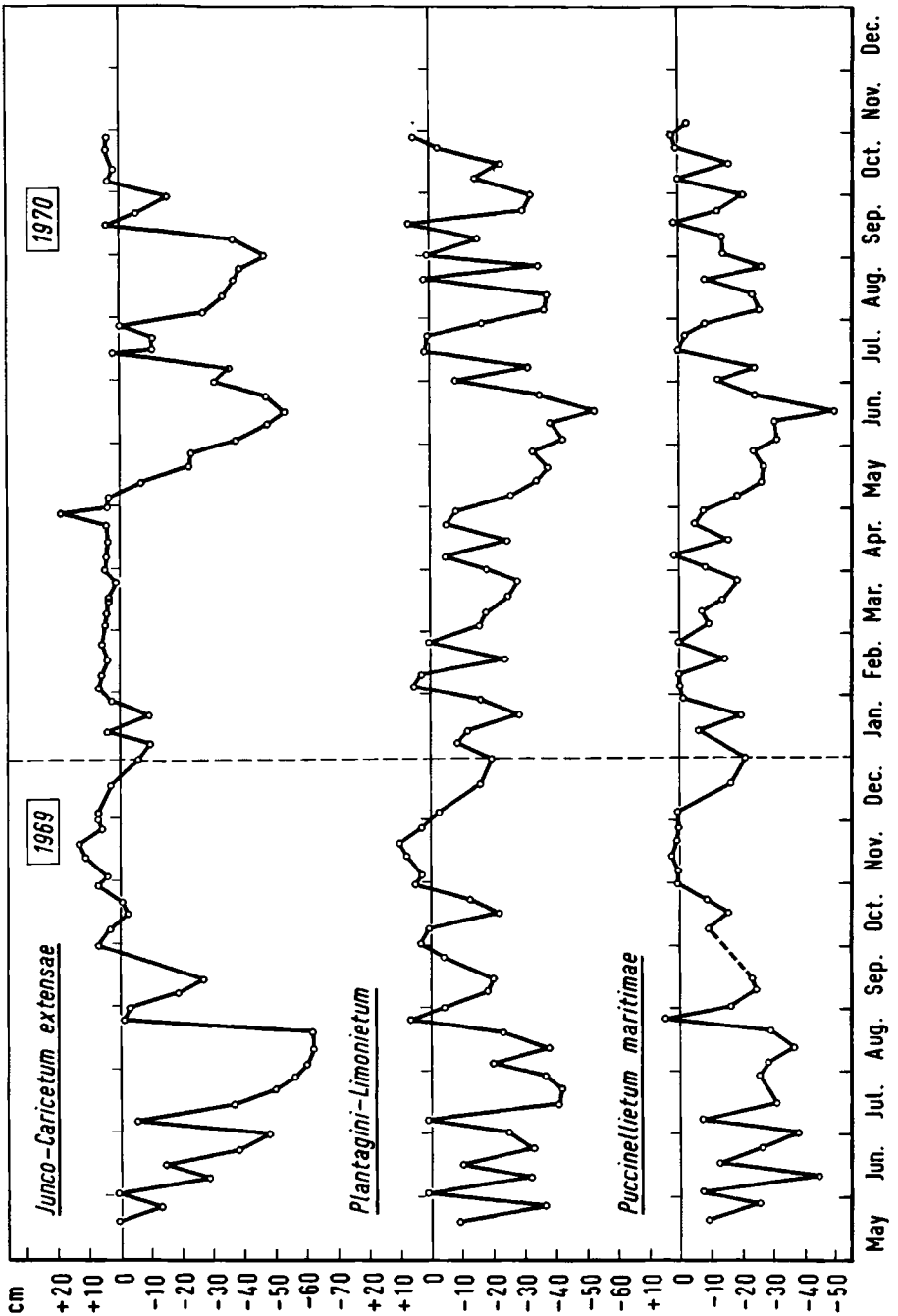

Fig.6. Changes in ground-water level in *Junco-Caricetum extensae* subass. *blysmetosum rufi*, *Plantagini-Limonietum* and *Puccinellietum maritimae*, in 1969 and 1970.

the influence of tidal movements on the ground-water levels. The reader is referred to Steggewentz (1933), Chapman (1960), Beeftink (1965) and Stoll (1965).

The following facts appear from the ground-water level curves shown in fig.6. JC is submerged from October to April. This is due to stagnation of flood-water as well as of rain-water; JC is usually flooded a few times during this period (see table 7). In addition, more rain falls in autumn and winter than in spring and summer. The ground water begins to decrease in May, not only because there is less precipitation, but also because evaporation and transpiration increase due to the rise in temperature (see table 2), the drawing out of the day and the sprouting of the vegetation. From May to October an increase in ground water in JC is caused by precipitation. The curves for precipitation and ground-water level show great similarity (cf. figs.5 and 6). As a result of rain-water draining from the surrounding dunes into JC, the increase in ground water is sometimes greater than the precipitation itself would imply.

The ground-water level curves for PL and PM are almost identical. As far as the months of May-September are concerned there is also some similarity with the curve for JC. The ground-water level in PM is generally somewhat higher than in PL (from April to October 1970 an average of 17.4 cm below the surface in PM; in PL an average of 23.8 cm below the surface). The variations in PM are, however, smaller than those in PL, probably due to the stronger influence of the ebb and flow of the tide (PM lies closer to the creek). During the vegetation season there are no prolonged floodings, while also in winter PL and PM can remain dry for long periods.

As a result of successive high floods, PL can remain inundated for some time (e.g. November 1969), while this is not so much the case with PM, due to the possibility of more rapid drainage. The influence of precipitation on the ground-water level is also present in PL and PM, although to a lesser extent than in JC because as has already been stated the influence of the tide on the ground-water level can be large in the first-mentioned areas.

SOIL-MOISTURE

Soil samples were collected for the determination of soil-moisture in the same way as those taken for the chemical analyses. In 1969 20 sub-samples, spread over the total vegetation, were taken. Because soil-moisture can vary greatly from place to place (see Verhoeven, 1953; Ranwell et al., 1964), 15 samples were taken in 1970, from a pre-determined place in the vegetation (in a row, with 2 m distance between them) in order to obtain more comparable data. During the vegetation period samples were taken every 2 weeks; several samples

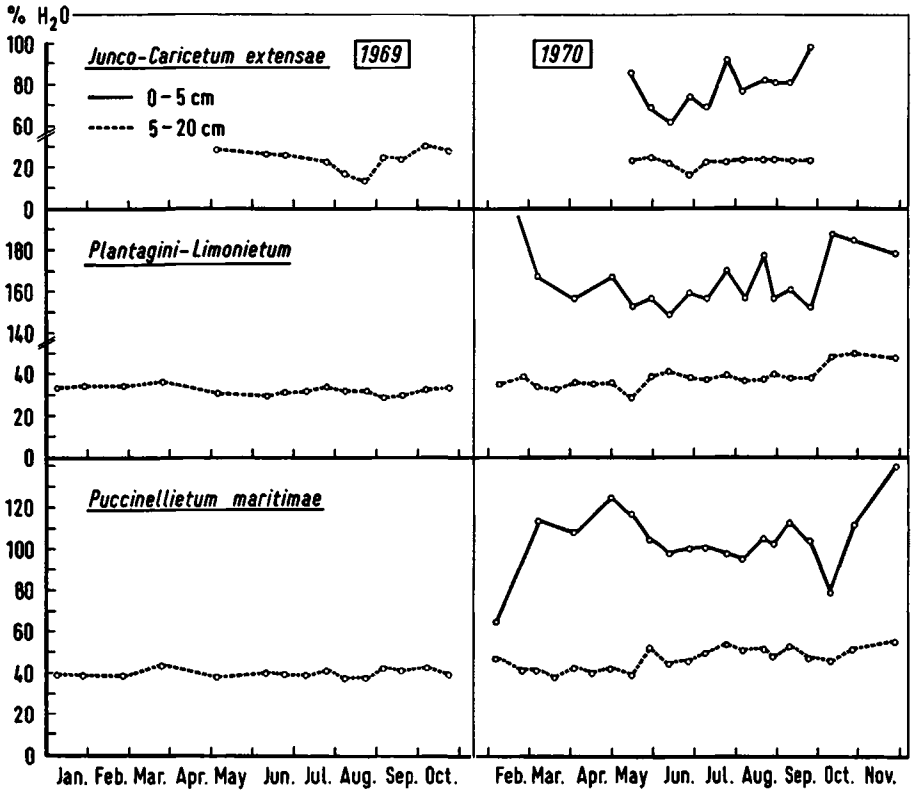

Fig.7. Soil moisture content in percentage by weight, of *Junco-Caricetum extensae* subass. *blysmetosum rufi*, *Plantagini-Limonietum* and *Puccinellietum maritimae* in 1969 and 1970

were also taken before and after this period. The soil samples were only collected when the experimental plots were not flooded. In 1969 only samples from the 5-20 cm layer were taken; in 1970 from the 0-5 cm 5-10 cm and 10-20 cm layers.

After the 15 to 20 sub-samples had been mixed well together, an amount of known weight (fresh weight) was taken from the mixture, dried at 105°C, and then re-weighed. The number of gms H_2O per 100 g oven-dry soil could thus be calculated. The results are given in table 8 and fig.7. It should be noted here that the values for the 5-20 cm layer in 1970 are calculated as the average of the values for the 5-10 cm layer and the 10-20 cm layer.

The moisture content of the 5-20 cm layer varies from 15%-35% in JC, from 30%-50% in PL and from 40%-55% in PM. It is relatively constant per layer. In JC the lowest values appear in the period with the lowest water-level (cf. fig.6); this is not the case with PL and PM.

The moisture content of the 5-20 cm layer is only slightly correlated with the

variations in ground-water level. During heavy surface evaporation in summer, there will be a sufficient amount of capillary rising water to ensure a constant soil-moisture content. In JC there is no difference in moisture content between the 5-10 cm layer and the 10-20 cm layer (see table 8), contrary to PL and PM, where the moisture content of the 5-10 cm layer is higher than that of the 10-20 cm layer. The moisture content in the 10-20 cm layer is very constant (25% in PL; 30%-35% in PM).

In the top layer the moisture content is much higher, and the fluctuations are more frequent. This layer, which contains organic material and silt, can hold more moisture than the underlying sand layer; however, the moisture content is more influenced by precipitation, evaporation and flooding. The moisture content is highest in the top layer of PL (150%-190%); it varies from 65%-140% in PM and from 60%-90% in JC. Samples can only be taken from JC over a short period of time. The lower moisture content in the top layer of PM, compared with that of PL is due to grazing, whereby the top layer is trampled down and the water content decreases.

A small rise in moisture content (5%-15%), occurs every month in the 0-5 cm layer of PL, followed by a decrease (see fig.7). This increase in soil-moisture content is always connected with the spring-tide period, when the ground-water level rises.

SALINITY OF THE SOIL-MOISTURE

The same samples used for determining the soil-moisture were used for determining the salinity, expressed in gms NaCl/l soil-moisture. The titration method according to Mohr (Steubing, 1965) was applied for this determination. In 1970 the soil samples were analysed in the laboratory of the Government Department for the IJsselmeerpolders in Baflo. During flooding of the studied sites, water samples were taken for NaCl determination. The results of the analyses are given in table 9 and fig.8.

The salinity depends upon evaporation, transpiration, precipitation, inundation and the stage of development of the soil. For data concerning the interaction of these factors, the reader is referred to Beeftink (1965).

In 1969 the salinity in the 5-20 cm layer of JC fluctuated between a minimum of 4 g NaCl/l and a maximum of 10 g NaCl/l. The low value in spring is due to the salt being leached by rain-water in the preceding months, when there was no flooding. In the spring of 1970 the salt content was higher, because the site was still flooded with sea-water in April. The maximum value for that year in the 5-20 cm layer was 18 g NaCl/l, the minimum amounted to 5 g/l. An increase in salt content occurs in periods of little or no precipitation when, as a

TABLE 8

Moisture content of the soil, in g H_2O/100 g oven-dry soil of three salt-marsh communities JC = Junco-Caricetum extensae subass. blysmetosum rufi; PL = Plantagini-Limonietum; PM = Puccinellietum maritimae

1969	Date	8-1	27-1	25-2	24-3	5-5	11-6	24-6	9-7	24-7
Site	Depth in cm									
JC	0-5									
	5-20					27.8	26.3	25.6		22.5
PL	0-5								171.4	
	5-20	33.5	34.1	34.3	36.3	30.5	29.5	30.8	31.4	33.5
PM	0-5								107.2	
	5-20	39.1	39.2	39.2	43.9	38.3	40.4	39.6	39.5	41.7
1970	Date	4-2	25-2	4/5-3	18-3	1-4	15-4	29-4	13-5	27-5
Site	Depth in cm									
JC	0-5								85.4	69.0
	5-10									25.4
	5-20								23.2	24.7
	10-20									24.0
PL	0-5	272.8		167.1		156.1		166.4	151.8	155.7
	5-10									51.7
	5-20	34.7	38.7	33.4	32.7	35.3	34.9	35.3	27.8	38.0
	10-20									24.3
PM	0-5	65.9		114.4		109.0		125.8	117.3	105.7
	5-10									76.2
	5-20	48.1	41.8	41.8	38.8	42.9	41.0	43.2	39.7	52.9
	10-20									29.5

result of evaporation, the soil dries up (low ground-water level, low moisture percentage).

The variations in salinity are greater in the top layer than in the 5-20 cm layer. In June 1970 the maximum salt content in JC was 19 g NaCl/l. In this dry period crystallisation of salts was noted; a white layer arose on the soil surface, especially on bare patches in the vegetation. Thus these crystallized salts no longer make up part of the soil-moisture. Since, however, they have been included in the soil samples, the measured salt concentration is probably somewhat too high from an ecological point of view. Salts are added by the capillary

7-8	22-8	4-9	18-9	6-10	23-10						
54.4				117.9							
16.3	12.8	24.4	23.5	30.4	27.6						
15.9				168.3							
31.3	31.3	28.5	29.3	31.9	33.2						
101.6				100.5							
37.3	37.3	42.4	41.5	43.3	39.5						
10-6	25-6	8-7	22-7	5-8	19-8	27-8	9-9	25/25-9	9-10	26-10	26-11
61.6	73.8/	69.0	92.1	76.3	81.7	80.7	80.4	97.4			
21.0	14.4	22.8	23.3	25.1	23.7	23.7	23.0	23.3			
21.3	15.8	22.4	22.6	23.7	23.4	23.4	22.4	23.3			
21.6	17.1	22.0	21.9	22.2	23.0	23.1	21.8	23.3			
148.4	159.0	156.0	170.1	156.0	176.5	156.2	160.6	152.2	187.6	184.9	177.7
57.7	52.4	49.7	56.2	50.2	48.7	54.2	52.3	52.1	71.7	76.8	67.5
40.8	38.2	37.1	39.5	36.5	36.8	39.3	37.8	38.2	47.8	50.0	47.5
23.8	23.9	24.4	22.8	22.8	24.8	24.4	23.3	24.3	23.8	23.1	26.6
99.0	101.1	101.9	98.5	96.2	106.1	104.1	113.9	104.8	80.4	112.8	141.4
60.6	65.0	70.0	75.1	67.1	70.7	66.3	73.0	66.0	65.8	74.0	80.6
45.4	47.2	50.6	54.4	51.8	52.6	48.8	53.9	48.7	47.0	53.0	56.4
30.2	29.4	31.1	33.7	36.5	34.5	31.3	34.7	31.4	28.1	31.9	32.2

rise of water. Due to precipitation in July 1970, the salt content in the top layer fell so sharply that a lower value was reached than in the 5-20 cm layer. Due to the leaching of salts from the top layer by rain-water, the salinity in the 5-20 cm layer falls much less. The NaCl content in the top layer remains lower than in the 5-20 cm layer until September. Floods occur in October; the NaCl content of the water samples then changes depending upon precipitation and upon new inundations.

The fluctuations in salinity in the top layer of PL and PM are much greater than in JC (PL 12-35 g NaCl/l; PM 11-54 g NaCl/l). The salinity curves of the

TABLE 9

Salinity, expressed in g NaCl/l soil moisture of three salt-marsh communities
JC = Junco-Caricetum extensae subass. blysmetosum rufi; PL = Plantagini-Limonietum;
PM = Puccinellietum maritimae
The values between brackets indicate water samples.

1969	Date	8-1	27-1	25-2	24-3	5-5	11-6	24-6	9-7	24-7	7-8	22-8
Site	Depth in cm											
JC	0-5										6.64	
	5-20					3.85	4.44	5.61		7.58	6.28	10.25
PL	0-5								16.64		29.39	
	5-20	15.73	12.50	16.04	15.28	18.04	16.61	17.48	22.37	18.52	19.38	24.53
PM	0-5								22.03		39.54	
	5-20	18.09	12.64	13.97	14.68	15.22	17.11	16.76	20.27	21.35	24.76	26.39
1970	Date	4-2	11-2	25-2	4/5-3	18-3	1-4	15-4	29-4 1-5	13-5	27-5	10-6
Site	Depth in cm											
JC	0-5		(7.0)	(7.7)	(5.3)	(5.6)	(11.9)		(13.5)	11.2	17.1	18.7
	5-10										14.6	19.5
	5-20									7.16	11.2	16.6
	10-20										7.8	13.7
PL	0-5	11.7	(19.3)	(7.4)	11.7		16.3		12.9	21.6	29.5	42.3
	5-10										21.0	24.2
	5-20	9.8		11.7	10.0	9.1	11.4	11.7	9.9	14.9	19.1	21.3
	10-20										17.1	18.4
PM	0-5	26.2	(17.2)	(8.0)	12.5		16.5		11.5	24.9	31.2	53.8
	5-10										18.8	23.4
	5-20	13.4		17.2	16.9	12.0	13.8	16.3	12.3	15.2	15.8	18.7
	10-20										12.7	13.94

biotopes, however, are very similar to each other (see fig.8). The highest values in PL and PM are also found in June, 42.3 g NaCl/l in PL and 53.8 g NaCl/l in PM. These are much higher concentrations than those in the flood-water. Capillary rise occurs here also due to evaporation, whereby salts are transferred from deeper layers, so that even with a slight drop in the moisture content (see table 8) the salinity increases considerably. Crystallisation of salt was observed on the surface of the soil in PM. In July the rain-water as well as the flood-water has a leaching effect in PL and PM. The highest salt content in the 5-20 cm layer is found at a later date than in the 0-5 cm layer. It is obvious that

4-9	18-9	6-10	23-10	12-11	20-11	27-11						
4.71	6.15	8.36	7.41	(16.07)	(21.16)	(6.07)						
18.88	19.73	20.73	22.89	(23.45)	(27.47)	(12.30)						
29.68	25.21		25.94	(22.63)	(23.94)	(13.12)						
25-6	8-7	22-7	5-8	19-8	27-8	9-9	24/25-9	9-10	23-10	26/29-10	26-11	16-12
19.2	5.30	1.36	3.02	6.33	6.57	8.28	2.49	(10.37)	(17.86)	(9.08)	(3.61)	(4.86)
16.2	8.3	(8.0)	5.9	7.2	8.6	10.1	4.9					
13.7	9.4	8.8	6.6	7.5	8.4	10.3	5.8					
11.2	10.5	9.5	7.2	7.8	8.2	10.5	6.8					
35.8	24.6	19.7	23.4	26.3	28.4	21.6	16.0	18.53		19.75	13.70	
27.8	10.72	20.4	21.0	24.6	23.6	30.0	15.0	19.13		20.31	17.2	
23.5	14.9	20.7	20.8	23.3	22.0	27.0	15.5	19.6		19.6	18.1	
19.2	19.1	20.9	20.5	21.9	20.3	24.1	16.07	19.96		18.94	18.9	
46.1	34.5	23.3	27.4	27.8	29.2	28.6	19.47	21.14		21.81	14.16	
28.2	33.4	27.9	24.4	25.5	27.5	29.9	20.98	21.75		22.60	19.1	
20.7	34.4	26.8	22.5	23.0	24.7	27.4	19.9	21.2		21.8	19.2	
13.17	35.3	25.7	20.6	20.5	20.8	24.9	18.82	20.69		20.97	19.3	

when the salinity in the top layer falls, due to leaching, this often first causes an increase in the salinity of the underlying layer before leaching also occurs from this layer.

The salinity in both soil layers of PL and PM is about the same until May and from September onwards. Regular flooding by sea-water keeps the salinity constant. During the vegetation season it is mainly the precipitation and evaporation which determine the salinity of the soil-moisture (see also Ranwell et al., 1964).

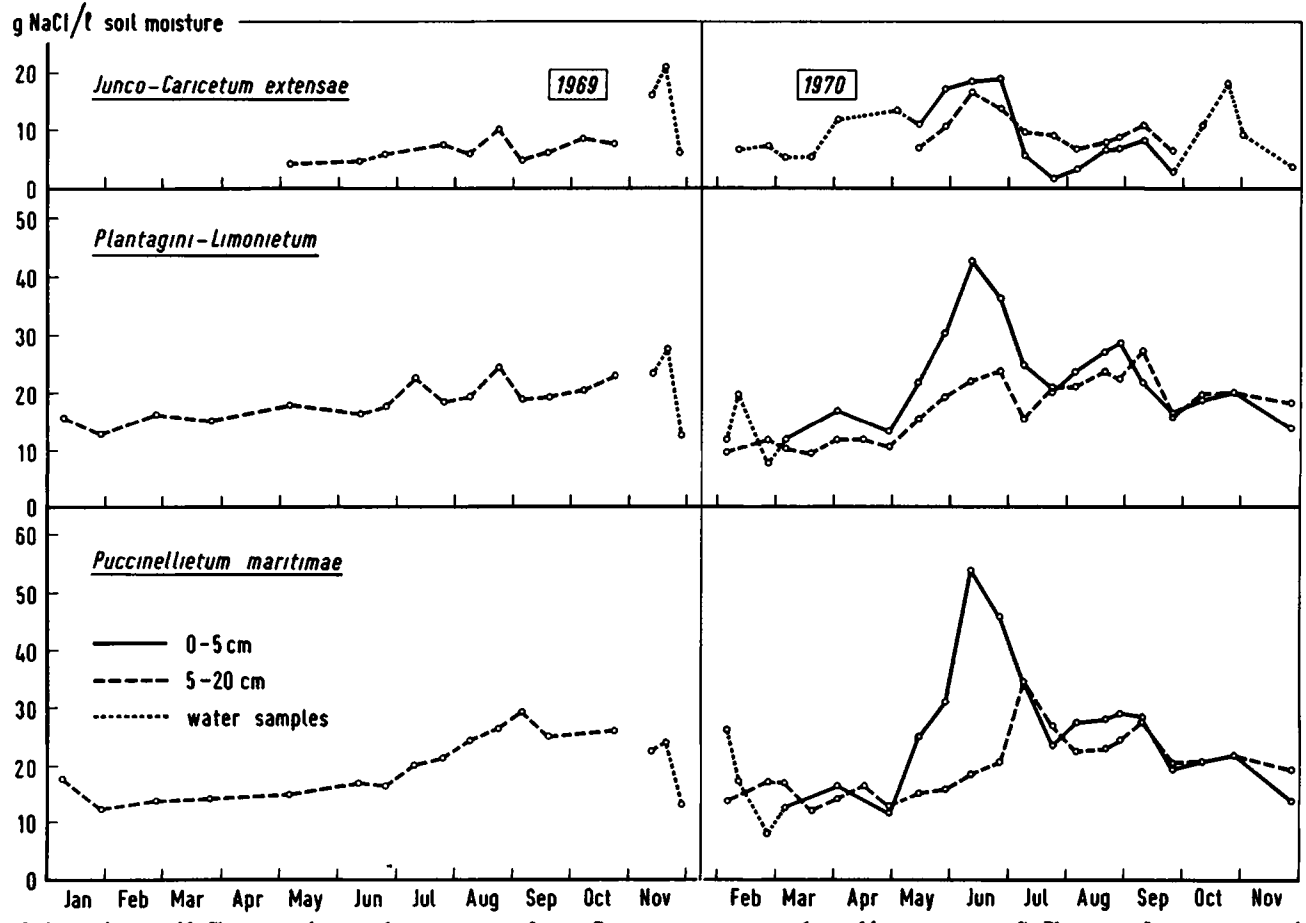

Fig 8 Salinity of the soil, in g NaCl to one litre soil moisture in *Junco-Caricetum extensae* subass *blysmetosum rufi*, *Plantagini-Limonietum* and *Puccinellietum maritimae* in 1969 and 1970

SEASONAL CHANGES IN STANDING CROP OF ABOVE-GROUND MATERIAL

Method

In order to be able to determine the changes in biomass of the above-ground plant material the harvesting method was applied. This method consists of the direct measurement of the standing crop of a previously specified area at different times. In the 3 plant communities, *Junco-Caricetum extensae* subass. *blysmetosum rufi*, *Plantagini-Limonietum* and grazed *Puccinellietum maritimae*, 10 plots were chosen before the beginning of the growing season (usually in March) and fenced off by vegetation cages. In 1967, cages covered by gauze on the upper side, and measuring 1 X 4 m, were used. After it became evident that such cages probably influenced the growth of the plants (cf. Daubenmire, 1940; Williams, 1951; Cowlishaw, 1955; Jagtenberg & De Boer, 1957), cages measuring 4 X 4 m were used in the following years and the upper sides were open.

Trampling by people and grazing by rabbits and cattle was prevented by these cages. The plots of 4 X 4 m (1967, 1 X 4 m) were not chosen at random in the communities, but attempts were made to choose areas which were as far as possible uniform, viz. from the point of view of floristic composition and coverage. Areas which were not representative of the site, such as bare spots, depressions, hummocks, transition zones or rabbit tracks, were avoided as far as possible. Care was taken to ensure that an experimental plot never occupied the same place twice. Because it was often difficult to judge the mentioned uniformity in spring, a provisional choice of the new plots for the following season was often made in autumn.

In 1967 a sample of 0.50 m was cut from each experimental plot every four weeks from April or May up to and including October. In order to avoid edge effects from cutting, circular samples (bounded by an iron ring) were taken, as demonstrated by Van Dyne et al. (1963). Each month a sample was taken from a different spot in the cage. Thus, 10 X 0.50 m^2 were harvested per month for each vegetation type. In order to study the development of the vegetation

under the influence of grazing by cattle, 10 samples (0.50 m^2 each) were also taken at random from outside the cages in PM. These are referred to as the PM-A samples.

In 1968 and subsequent years, circular samples of 0.125 m^2 were cut each month. In JC and PL the number of samples per harvest was increased to 15. Two samples were now taken alternately from 5 of the 10 experimental plots. When two samples were taken from one cage they were chosen as far away as possible from each other, and in any case with a distance between them of at least 2 m. During bad weather or bad site conditions only 10 samples were harvested at a time. Care was always taken to harvest at a distance of at least 50 cm from the side of the cage in order to avoid the edge effects of the cages. Due to the greater uniformity of PM, compared with that of JC and PL, it was not considered necessary to increase the number of samples in PM. It is beyond the scope of this publication to go into the relationship between the number and size of the samples, and the determinations of the biomass. The reader is referred to Christides (1931), Wiegert (1962), Van Dyne et al. (1963) and Miller & Hughes (1968).

All green plant parts were cut from each sample of 0.125 m^2 (in 1967, 0.50 m^2) to ground level, using scissors. At the same time all the dead plant material, that lying loose on the ground as well as the standing dead parts, was collected. The total amount of biomass collected in this way was placed in plastic bags, a separate bag being used for each sample. When the material could not be treated immediately it was deep frozen.

The treatment of the samples was carried out in the following way: The collected material was sorted into living (green parts) and dead material. The living material was then split up into species and occasionally a further distinction was made between the leaves and flowering parts of one species. When necessary, for example after harvesting in very wet sites, all the material, or only the dead, was rinsed over a sieve in order to remove the sand and silt. During sorting all the dead material, that is the dead plant remains from the previous year as well as the dead parts formed during the year in question was usually combined together. In 1970 attempts were made to separate the old dead material from the newly-formed in the JC and PL samples. So little old dead material was present in the PM and PM-A samples that separation was not considered necessary in this case.

The sorted material was dried for at least 12 hours at 85°C in a force-draught oven and then weighed to within an accuracy of 0.01 g. The average values of the biomasses were expressed in g/m^2.

All the samples were initially sorted in the way described above. This was very time-consuming, especially as far as the PM and PM-A samples, which often had very minute plant parts, were concerned. Several modifications were, therefore,

introduced in the sorting procedure. In 1969 and 1970 the PM-A samples, which were the most difficult to sort, were first weighed (fresh weight) and then a sub-sample of known weight was taken from each sample; these sub-samples were dried and weighed in order to determine the total dry weight of each sample. After these sub-samples had been taken the rest of the material was put together and mixed well; 10 samples were taken from this mixture in order to determine the floristic composition and the amount of dead material (cf. Welch & Rawes, 1965).

The forementioned modification was not applied to the JC, PL and PM samples, because it was not absolutely certain whether the results obtained in this way were comparable with those of the previous years.

Experiments with the PM samples showed that the percentage of dead *Puccinellia maritima*, with respect to the total amount of *Puccinellia* – dead and living – was rather constant per month. Consequently it was assumed that it was no longer necessary to sort the 10 samples completely. A distinction therefore was made between the green parts of the separate species, the dead material, and the total material (dead plus living) of *Puccinellia maritima*. Experimental experience showed that it was sufficient to sort half of the *Puccinellia* material from only 5 samples into dead and living parts. Weight percentages were calculated and applied to the total amount of *Puccinellia maritima*. The PM samples in 1970 were sorted in this way.

Only 10 of the 15 samples from JC and PL were sorted per month in 1970, after it had been shown from data of previous years that the average weight percentages of the dead material, and of the separate species of 10 samples, scarcely differed with the corresponding percentages of 15 samples.

Phenological observations were carried out on the plants on the days of sampling, in order to correlate the changes in standing crop with the different development stages of the plants.

From the changes in standing crop, estimations were made in different ways of the total net primary production of the three studied sites, during the years of investigations. At the same time growth rates, expressed in $g/m^2/day$, were calculated for each harvest period.

In order to study the development of the vegetation during prolonged periods without grazing, a small area of 10 X 10 m was marked off in *Puccinellietum* in April 1968 and kept completely free from grazing. In September 1970, and August and September 1971, a few samples of 0.125 m^2 were harvested from this plot. The material was then treated according to the method described above.

In 1970 the above-ground production of the grazed area was also determined by the use of movable vegetation cages of 1 X 4 m. The procedure was as follows: After the first month of grazing (end of June) cages were placed over

plots, from which a sample of 0.125 m^2 was first harvested in order to determine the standing crop. After about 4 weeks another sample of 0.125 m^2, bordering on the previous one, was cut from each cage. At the same time another sample was cut, at a distance of ± 3 m from the cage; the cage was then placed over it. The production during the period between two harvests was calculated from the difference in the average yield in the cages and the yield of the previous harvest outside the cages (Welch & Rawes, 1965). Eight cages were used, so 8 X 0.125 m^2 were harvested per sampling date. The cages could be transferred four times during the period from July up to and including September

Finally, living material from a few samples from the 1967 and 1968 seasons was chemically analysed, and the contents of crude protein, crude fibre and crude ash were determined. These analyses were carried out in the Laboratory for Soil and Crop Testing in Oosterbeek.

Results

JUNCO-CARICETUM EXTENSAE SUBASS. BLYSMETOSUM RUFI

Table 10 gives the average values of the standing crops in g/m^2 of the total above-ground material, the living and dead material separately, and each of the various species. At the same time, the percentages in regard to the total biomass are calculated for the living and dead material, while the percentages in regard to the living biomass are reported for the species. The changes in dead and living material with time are given in fig.9.

Dead material

The sampling of dead material in spring and autumn brought about many difficulties whenever the area was very wet. It was not always certain whether all the material had been collected. This should therefore be taken into account when considering the values.

The curves of the dead material for the various years show little agreement (see fig.9). The amount of dead material fluctuates during the season. The highest values are found in spring and autumn, but the fluctuations between those times are large and they are dependent upon the decomposition of old, dead plant remains and the mortality of the green material. After October the amount of dead material will rise even more as, due to unfavourable weather conditions (rain, flooding, frost), all the living material dies off.

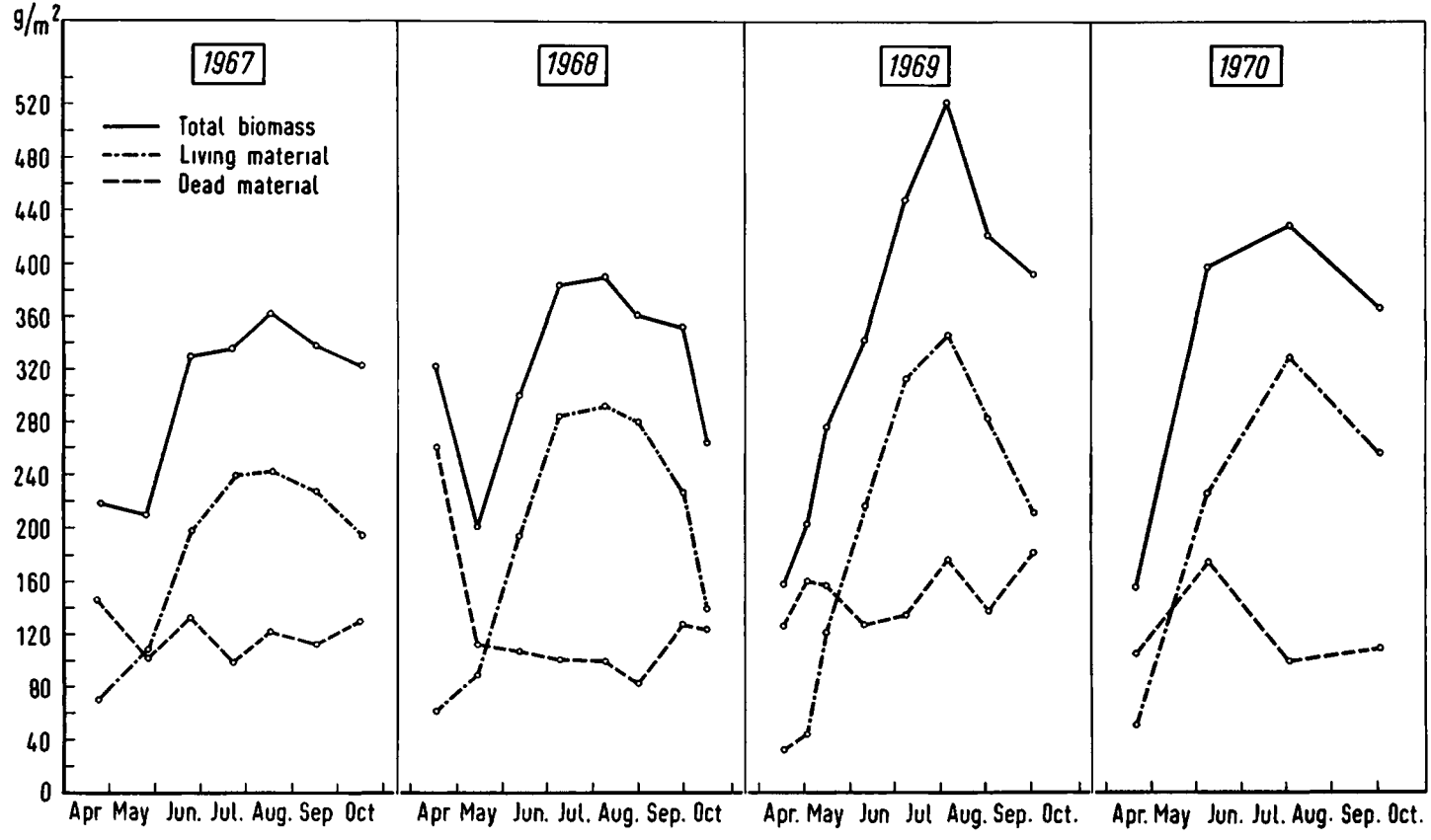

Fig.9. Changes in standing crop of above-ground material in *Junco-Caricetum extensae* subass. *blysmetosum rufi*, from 1967 to 1970 inclusive

TABLE 10

Changes in standing crop of dead material, living material and total vegetation in g/m^2 and in percentage of weight of total biomass, in *Junco-Caricetum extensae* subass. *blysmetosum rufi*

Also the portion of the various species in g/m^2 and in percentage of weight of the living material

Percentages less than 0.5 are not given.

Year	1967									
Date	Apr.24th		May 25th		June 22nd		July 20th		Aug.16th	
	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%
Total biomass	218.85		212.49		331.73		338.36		363.23	
Dead material	146.60	*67.0*	103.01	*48.5*	132.24	*39.9*	97.60	*28.8*	120.16	*33.1*
Living material	72.25	*33.0*	109.48	*51.5*	199.49	*60.1*	240.76	*71.2*	243.07	*66.9*
Species:										
Juncus gerardii	14.48	*20.0*	34.58	*31.6*	73.61	*36.9*	89.38	*37.1*	86.07	*35.4*
Plantago maritima	24.17	*33.5*	38.71	*35.4*	43.17	*21.6*	56.37	*23.4*	79.16	*32.6*
Triglochin maritima	1.16	*1.6*	3.03	*2.8*	5.20	*2.6*	5.41	*2.2*	5.25	*2.2*
Scirpus rufus	9.46	*13.1*	19.32	*17.6*	51.30	*25.7*	60.92	*25.3*	38.36	*15.8*
Carex extensa	15.56	*21.5*	9.88	*9.0*	21.46	*10.8*	22.71	*9.4*	26.81	*11.0*
Agrostis stolonifera var. compacta subvar. salina	3.61	*5.0*	1.73	*1.6*	1.86	*0.9*	1.45	*0.6*	3.73	*1.5*
Limonium vulgare	0.20		0.04		1.12	*0.6*	0.42		0.48	
Armeria maritima	0.89	*1.2*	0.87	*0.8*	0.48		0.69		1.20	*0.5*
Festuca rubra f. litoralis	0.09				0.15		0.83		0.18	
Eleocharis palustris ssp. uniglumis			0.15		0.01		0.03			
Centaurium pulchellum							0.06		0.17	
Odontites verna ssp. serotina										
Parapholis strigosa					0.13		0.36		0.31	
Glaux maritima			0.05		0.34		0.13		0.07	
Puccinellia maritima	+		0.04		0.05		0.01		0.06	
Aster tripolium					+		0.01			
Salicornia europaea									+	
Suaeda maritima										
Artemisia maritima										
Halimione portulacoides										
Atriplex hastata										
Scirpus maritimus										
Juncus maritimus										
Juncus articulatus	0.14		0.04		0.21		0.89		0.28	
Juncus alpino-articulatus ssp.atricapillus							+		+	
Phragmites australis							+			
Schoenus nigricans							0.73		0.02	
Hippophaë rhamnoides										
Leontodon autumnalis									0.02	
Potentilla anserina										
Moss spec.	0.35	*0.5*	0.14				+			
Not det.	2.13	*2.9*	0.89	*0.8*	0.42		0.35		0.18	

1968													1969									1970				
Sep.14th	Oct.16th	Average	Apr.17th	May 14th	June 10th	July 8th	Aug.5th	Sep.2nd	Sep.30th	Oct.16th	Average	Apr.16th	May 2nd	May 14th	June 10th	July 8th	Aug.5th	Sep.2nd	Oct.3rd	Average	Apr.24th	June 8th	Aug.3rd	Oct.1st	Average
g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %
338.74	322.98	303.77	322.69	200.11	298.97	385.44	391.19	361.53	353.38	263.66	322.12	155.96	200.94	274.75	341.14	444.74	519.84	418.33	390.50	343.28	153.90	396.57	428.38	366.40	336.31
111.72 *33.0*	129.12 *40.0*	120.06 *39.5*	262.08 *81.2*	113.43 *56.7*	106.77 *35.7*	101.07 *26.2*	100.08 *25.6*	82.22 *22.7*	127.54 *36.1*	123.86 *47.0*	127.13 *39.5*	125.01 *80.2*	158.76 *79.0*	155.90 *56.7*	125.08 *36.7*	132.75 *29.9*	173.84 *33.4*	135.06 *32.3*	180.17 *46.2*	148.32 *43.2*	103.48 *67.2*	171.91 *41.7*	99.64 *33.3*	110.10 *30.1*	121.28 *36.0*
227.02 *67.0*	193.86 *60.0*	183.71 *60.5*	60.61 *18.8*	86.68 *43.3*	192.20 *64.3*	284.37 *73.8*	291.11 *74.4*	279.31 *77.3*	225.84 *63.9*	139.80 *53.0*	194.99 *60.5*	30.95 *19.8*	42.18 *21.0*	118.85 *43.3*	216.06 *63.3*	311.89 *70.1*	346.00 *66.6*	283.27 *67.7*	210.33 *53.8*	194.96 *56.8*	50.42 *32.8*	224.66 *58.3*	328.80 *76.7*	256.30 *69.9*	215.05 *64.0*
74.27 *32.7*	62.80 *32.4*	62.17 *33.8*	12.78 *21.1*	33.65 *38.8*	82.42 *42.9*	137.10 *48.2*	126.16 *43.3*	124.36 *44.5*	83.69 *37.1*	55.24 *39.5*	81.93 *42.0*	8.36 *27.0*	20.93 *49.6*	47.31 *39.8*	91.70 *42.4*	134.53 *43.1*	139.61 *40.3*	106.02 *37.4*	79.35 *37.7*	78.48 *40.2*	16.59 *32.9*	145.06 *64.6*	212.87 *64.7*	133.37 *52.1*	126.97 *59.1*
84.14 *37.1*	67.46 *34.8*	56.17 *30.5*	32.69 *53.9*	36.91 *42.6*	66.43 *34.6*	87.38 *30.7*	87.47 *30.0*	83.84 *30.0*	60.38 *26.7*	14.50 *10.4*	58.70 *30.1*	8.02 *25.9*	6.16 *14.6*	40.49 *34.0*	64.93 *30.1*	78.16 *25.1*	106.93 *30.9*	89.49 *31.6*	68.94 *32.8*	57.89 *29.7*	24.68 *48.9*	49.13 *21.9*	76.84 *24.0*	86.29 *33.7*	59.24 *27.6*
4.51 *2.0*	5.84 *3.0*	4.34 *2.4*	0.82 *1.4*	4.26 *4.9*	8.37 *4.4*	10.57 *3.7*	10.14 *3.5*	9.91 *3.5*	6.14 *2.7*	3.32 *2.4*	6.69 *3.4*	0.20 *0.6*	1.50 *3.6*	5.39 *4.5*	10.42 *4.8*	14.49 *4.7*	10.65 *3.1*	6.88 *2.4*	4.24 *2.0*	6.72 *3.4*	1.67 *3.3*	19.23 *8.6*	16.79 *5.1*	10.33 *4.0*	12.01 *5.6*
25.41 *11.2*	13.80 *7.1*	31.22 *17.0*	3.22 *5.3*	6.01 *6.9*	24.52 *12.8*	32.33 *11.4*	39.04 *13.4*	33.16 *11.8*	41.55 *18.4*	28.68 *20.5*	26.06 *13.4*	1.90 *6.1*	4.58 *10.9*	9.17 *7.7*	32.26 *14.9*	52.57 *16.9*	40.24 *11.6*	29.45 *10.4*	20.47 *9.7*	23.83 *12.2*	3.54 *7.0*	6.44 *2.9*	5.65 *1.7*	5.39 *2.1*	5.26 *2.4*
27.18 *12.0*	16.98 *8.8*	20.08 *10.9*	7.16 *11.8*	3.87 *4.5*	6.69 *3.5*	10.82 *3.8*	15.60 *5.4*	11.34 *4.1*	23.36 *10.3*	28.14 *20.1*	13.37 *6.9*	10.42 *33.7*	8.36 *19.8*	13.42 *11.3*	13.26 *6.1*	22.40 *7.2*	32.16 *9.3*	30.82 *10.9*	26.19 *12.5*	19.63 *10.1*	3.05 *6.0*	1.48 *0.7*	3.33 *1.0*	4.10 *1.6*	2.99 *1.4*
8.84 *3.9*	20.86 *10.8*	6.01 *3.3*	3.19 *5.3*	1.21 *1.4*	1.75 *0.9*	3.45 *1.2*	6.66 *2.3*	8.43 *3.0*	7.87 *3.5*	6.29 *4.5*	4.86 *2.5*	2.04 *6.6*	0.42 *1.0*	1.95 *1.6*	1.23 *0.6*	2.80 *0.9*	7.31 *2.1*	6.53 *2.3*	8.63 *4.1*	3.86 *2.0*	0.86 *1.7*	2.57 *1.1*	5.74 *1.7*	12.46 *4.9*	5.41 *2.5*
0.56	0.08	0.41	0.17	0.21	0.62	0.42	0.45	0.55	0.67	0.04	0.39		0.07	0.25	1.05 *0.5*	1.75 *0.6*	0.58	0.82	0.02	0.57		0.25	2.91 *0.9*	+	0.79
0.16	1.19 *0.6*	0.78			0.39	0.03					0.05	+		0.22		0.66	0.01	1.45 *0.5*		0.29					
0.27	0.32	0.26			0.05	0.01		0.03	0.03	+	0.02			0.25	0.14		0.23	1.19	0.18	0.25			1.54 *0.5*		0.39
		0.03		0.11	0.45	0.14	1.89 *0.6*	0.29		0.25	0.39			0.10	0.29	1.15	0.29	2.06 *0.7*	0.07	0.50	0.03	0.33	0.94	0.17	0.37
0.17	0.05	0.06				0.04	0.70	1.34 *0.5*	0.69	0.05	0.35			+	+	0.19	0.95	0.80	0.07	0.25			0.04	2.60 *1.0*	0.66
0.21		0.03				0.01		0.22			0.03			0.01	0.04	2.09 *0.7*	4.48 *1.3*	6.27 *2.2*	0.22	1.64 *0.8*				0.01	+
0.02	0.10	0.13				0.04	+	0.01		0.02	0.01					0.19	0.52	0.07		0.10 *0.5*					
0.27	0.62	0.21	0.01		0.39	1.67 *0.6*	1.50 *0.5*	4.94 *1.8*	0.98	2.42 *1.7*	1.49 *0.8*	+	0.02	0.25	0.64	0.61	0.81	1.26	0.90	0.56	+	0.15	0.98	0.33	0.37
0.03	0.28	0.07		+	0.02	+	+				+			0.04	0.03				0.02	0.01			0.01	0.68		0.17
+		+											0.14							0.02			0.01	0.34	1.21 *0.5*	0.39
0.01		+		0.01							+					+		+		+			0.09	0.04	0.03
0.16		0.02																+		+		+	+		+
																+				+					
																	+			+					
																		0.06		0.01					
	1.95 *1.0*	0.28					0.34	0.02			0.05						0.33			0.04					
							0.02				+														
0.24	0.24	0.29			0.09	0.34	0.17				0.08						0.21			0.03					
+		+					0.84	0.78	0.14	0.99 *0.7*	0.34				0.03	⎧ 0.30	0.58		0.43	0.16					
		+														⎩									
0.02		0.11																							
																+	0.02	0.01		+					
0.03	0.03	0.01					0.01	0.02	+		+					+			+	+					
																	+	0.06	0.57	0.08					
0.15	0.11	0.11						0.04	0.33		0.05						0.09	+		0.01			+		+
0.37	1.13 *0.6*	0.78	0.51 *0.8*	0.07	+	+	+				0.07														

At the beginning of the season the amount of dead material is much greater than the living biomass (April 67%-80% of the total biomass), but during the course of the season this percentage falls. It reaches its lowest value in the middle of the summer (23%-30% of the total biomass).

TABLE 11
Changes in biomass of dead material
in *Junco-Caricetum extensae* subass. *blysmetosum rufi* (Values in g/m^2)

1970		April	June	August	October
total	dead material	104	172	100	110
old	dead material	104	157	77	
newly-formed	dead material		15	23	

Table 11 gives the amounts of old and newly-formed dead material in JC in 1970, in g/m^2.

This shows that the mortality of the living material in spring and early summer is limited. The old dead material decreases in the summer. Unfortunately, it was impossible to make further distinction in October between recent dead material and the dead material of the previous years. It is to be expected that the old, dead material has decreased even more and that the new has increased. The increase in old dead material from April to June, can presumably be explained by an error during harvesting of the wet material in April.

Living material

The changes in standing crop of the living material give an accurate picture of the development of the vegetation in the course of a year. At the beginning of the vegetation period there is only little green material present. The differences in living biomass in April between the four separate years are mainly due to weather conditions in the weeks preceding harvesting. The beginning of spring in 1968 was relatively warm, with little precipitation; plant growth began rather early; on April 17th there was already 60 g/m^2 of green biomass (dry weight). The spring of 1969, on the other hand, was cold and at the time of the first harvest only 30 g/m^2 was present. The same applies for 1967 (higher temperatures – more biomass) and 1970 (lower temperatures – less biomass). The amount of green parts increases quickly until the maximum is reached in August. The maximum values vary from 243 g/m^2 in 1967 to 346 g/m^2 in 1969, with intermediate values for the other years (see table 10). The biomasses in July and September 1967-1968 often differ only slightly from the maximum values. The peak seems to continue for a longer time. In 1969 a very sharp fall is observed after the maximum (see fig.9). This is also the case in 1970, but this time it must be taken into account, that the intervals of time

between 2 harvests were much greater than in the other years. The curve showing the development of the green material is possibly, therefore, not completely accurate, even though it is similar to that of 1969. The living biomass decreases quickly after August-September, and in the winter falls to values which are presumably lower than those of the coming spring.

From the values of the dead and living biomass it can be seen that the living material fluctuates more during the season than the dead material. The maximum values for the living biomass are 5-10 times greater than the minimum values. Except in spring, there is always more living material present than dead material. The shape of the curve for the total biomass (dead and living) is similar therefore to that of the living material (see fig.9).

Floristic composition

Of the 31 species found in JC during the years of investigation, only 6 form together 90%-95% of the living biomass (see table 10) The rest of the biomass is divided between an average of 10 other species per harvest. The 6 main species are *Juncus gerardii, Plantago maritima, Scirpus rufus, Triglochin maritima, Carex extensa* and *Agrostis stolonifera.* The first two of these are the most important; together they constitute 60%-88% of the living material. The proportion of each of these main species varies during the growing season, depending upon the development of each species. Of those species which make up a small part of the total biomass, there are a few which have only been found once or twice (e.g. *Phragmites australis, Artemisia maritima, Halimione portulacoides*), while the others were found regularly in the samples, but in very small quantities (see table 10). The changing size of the population of the annual species such as for example *Salicornia europaea, Centaurium pulchellum* and *Odontites verna* can also easily be seen in table 10. In 1969 *O. verna* was very prevalent in the area and in August of that year this population accounted for more than 2% of the total, living biomass. In other years the species was present, but found less frequently and with reduced vitality. In 1970 many, although small, *Sal. europaea* plants were found, probably due to a spring-tide which inundated JC at the end of April. Seeds of *Salicornia* were carried along which germinated in May under favourable conditions brought about by the preceding flood. Fig.10 shows graphically the changes in biomass of a few of the most important species. The difference in development of each species is clearly seen. *J. gerardii* usually reaches its maximum value in July-August. This maximum, however, can sometimes be maintained, with slight fluctuations, until September. The maximum falls during fruit setting after a period of optimum flowering. *J. gerardii* usually has a short flowering period which lies between the beginning of June and the beginning of July. The maximum biomass of *J. gerardii* amounted to 89 g/m^2 in July 1967, 137 g/m^2 in July 1968,

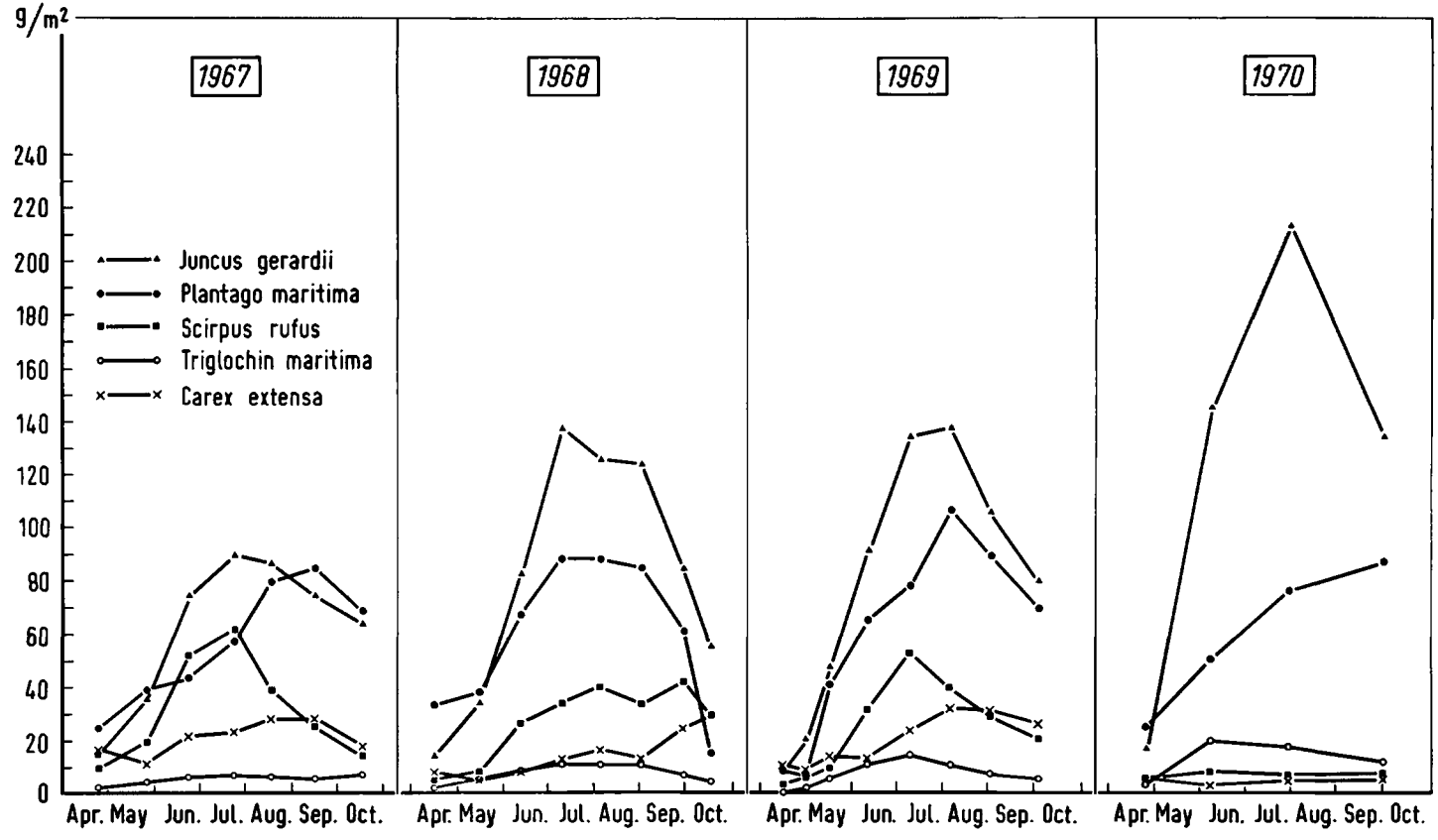

Fig.10. Changes in standing crop of important species in *Junco-Caricetum extensae* subass. *blysmetosum rufi*, from 1967 to 1970 inclusive

140 g/m^2 in August 1969 and 213 g/m^2 in August 1970. Table 12 gives the biomasses of the leaves and flowering stalks of *J. gerardii* separately.

TABLE 12
Changes in biomass of the leaves and the flowering stalks of *Juncus gerardii* (Values in g/m^2)

1970	April 24th	June 8th	August 3rd	October 1st
total biomass	17	145	213	133
leaves	17	139	149	81
flowering stalks		6	64	52

This table shows that leaf growth after June is limited, while in the June-August period the flowering parts increase greatly in weight and finally form 30% of the biomass. Optimum flowering occurs at the end of June, and fruit setting and ripening takes place in July. Much of the leaf dies off in October, but most of the flowering stalks, with ripe seed capsules, still remain on the plant and must be considered as 'living' material. Only a small part of the seed is lost by falling to the ground or by consumption.

The standing crop curves for *Plantago maritima* are very similar, even though the time at which the maximum amount is achieved varies from the beginning of July to October (see fig.10 and table 10). The maximum in October 1970 is probably not real. The maximum yield is relatively constant and varies from ± 85 g/m^2 (1967, 1968 and 1970) to 107 g/m^2 (1969). The mortality of the leaves of *Pl. maritima* can be high during the season, especially during flowering and fruit setting so that the biomasses remain almost constant for longer periods as was the case in 1967 and 1968.

The maximum biomass of *Scirpus rufus* is also reached just after flowering and seed development (July). From August onwards a re-growth is often evident in *S. rufus*. Due to this there is again an increase in material and a second peak is reached at the end of September in 1968 (see fig.10). The plants can occasionally even flower again in September, as was noted in 1966. In other years (1967 and 1969) this re-growth is less, and is overshadowed by decay and seed loss. In these years the biomass did not increase after August.

As a result of the usually small biomasses of *Triglochin maritima* and *Carex extensa* the latter of which in addition is irregularly found in clumps, monthly differences in weight of these species can hardly be ascertained. Even so both species show a development towards a maximum and then again a decrease; this can be seen especially in *Tr. maritima* in 1969 and 1970. *C. extensa* usually has a peak late in the season.

Table 10 en fig.10 indicate that during the years 1967-1970 the average biomass of *J. gerardii* has increased greatly, while that of *C. extensa* and

S rufus have decreased, particularly in the last year *Tr maritima* also shows a certain increase. The biomass of *Pl maritima* on the other hand is more or less constant over the years (see also discussion).

TABLE 13

Frequency of occurrence of the species (in percentages) in the total number of cut samples (of 0.125 m^2, 1967 of 0 50 m^2) in *Junco-Caricetum extensae* subass. *blysmetosum rufi*

	1967	1968	1969	1970
Total number of cut samples	70	115	100	45
Juncus gerardii	100	100	98	100
Plantago maritima	93	96	96	100
Triglochin maritima	100	100	100	100
Scirpus rufus	99	96	97	71
Agrostis stolonifera subvar salina	98	96	91	87
Carex extensa	89	88	86	64
Festuca rubra f litoralis	47	10	25	9
Glaux maritima	40	37	51	38
Limonium vulgare	33	44	35	9
Centaurium pulchellum	32	36	40	24
Puccinellia maritima	23	4	7	9
Juncus articulatus	21	5	2	–
Armeria maritima	13	2	8	–
Parapholis strigosa	13	4	12	2
Leontodon autumnalis	10	6	4	–
Eleocharis palustris ssp. uniglumis	4	19	16	22
Aster tripolium	3	(1)	3	11
Salicornia europaea	3	2	5	22
Schoenus nigricans	3	–		–
Phragmites australis	3	–	–	–
Suaeda maritima	1	–	1	4
Odontites verna ssp. serotina	1	4	32	2
Scirpus maritimus	1	(1)	–	–
Moss spec.	20	(1)	1	–
Juncus alpino-articulatus ssp. atricapillus	–	10	7	–
Juncus maritimus	–	(1)	–	–
Artemisia maritima	–	–	3	–
Halimione portulacoides	–	–	1	–
Potentilla anserina	–	–	3	–
Hippophae rhamnoides	–	–	2	–
Atriplex hastata			1	–

The frequency of occurrence of the species in the samples of each sampling date was determined during sorting. Frequency percentages for each species were calculated from the total number of samples taken per season. A comparison of these percentages, which are given in table 13, with the data from

table 10, shows that a few species such as *J. gerardii* and *Tr. maritima*, which have increased in weight, were not more frequently found in the samples. They must have developed therefore into more and/or larger plants. *S. rufus* and *C. extensa* on the other hand, have not only decreased in weight but also occurred less frequently in the samples (*Scirpus* 96% in 1968, 71% in 1970; *Carex* 88% in 1968, 64% in 1970). There is, therefore, a clear decrease in the number of plants per unit area. The fluctuations in frequency percentages of the annual species (such as e.g. *C. pulchellum O. verna* and *Sal. europaea*) are similar to the changes in biomass.

The decrease in the number of incidental taxa must partly be attributed to the limited sampling of 1970.

PLANTAGINI-LIMONIETUM

The PL area was harvested for three consecutive years. The values for all the found biomasses are given in table 14. Fig.11 shows the curves for the dead and living material and the total material. In April 1969 the material could not be sorted as harvesting took place under very wet conditions and very little green material was present. In April 1970 harvesting could not take place at all due to flooding.

Dead material

The fluctuations in dead material in PL are similar from year to year (see fig.11). There is a decrease in dead material at the beginning of the growing season due to rapid decomposition; there is no, or very little, mortality of green parts at that time. After a minimum value has been reached, a gradual almost linear increase in dead material takes place. The highest values are found in October. The proportion of dead material in the total biomass is greatest in spring and autumn (50%-80%), the smallest in July (21%-32%). The amount of dead material in spring differs from year to year and is dependent upon the production of the previous year, the rate of decomposition and the disappearance of material as a result of flooding in the winter months. There was a small amount of dead material in the spring of 1968. Due to favourable weather conditions at that time, and maybe also in autumn 1967, a great deal of material had already decayed. The springs of 1969 and 1970 were cold; there was little decomposition of dead material before May; a great deal of dead biomass was still present in May 1969 and 1970. Moreover, the increase in dead material in 1968 was relatively greater than in the subsequent years.

TABLE 14

Changes in standing crop of dead material, living material and total vegetation in g/m^2 and in percentage of weight of total biomass, in *Plantagini-Limonietum*

Also the portion of the various species in g/m^2 and in percentage of weight of the living material

Percentages less than 0.5 are not given.

Year	1968									
date	Apr 24th		May 21st		June 17th		July 15th		Aug 12th	
	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%
Total biomass	187 12		207.90		389.47		472,68		602 81	
Dead material	113.36	*60.6*	71.10	*34.2*	94.80	*24.3*	100 18	*21.2*	137 10	*22 7*
Living material	73.76	*39 4*	136.80	*65 8*	294.67	*75 7*	372 50	*78 8*	465 71	*77 3*
Species										
Plantago maritima	57 60	*78.1*	80.56	*58.9*	180.99	*61.4*	243.90	*65 5*	330.87	*71 0*
Limonium vulgare	7.58	*10.3*	34.51	*25.2*	68.09	*23.1*	89.54	*24.0*	94.17	*20 2*
Triglochin maritima	1.29	*1 7*	4.70	*3.4*	13.54	*4.6*	8 12	*2 2*	8 72	*1 9*
Aster tripolium	1.71	*2 3*	3.40	*2.5*	3.69	*1 3*	5 42	*1.5*	5 63	*1.2*
Festuca rubra f litoralis	0.51	*0.7*	2.27	*1 7*	5.47	*1.9*	9.76	*2 6*	4.03	*0 9*
Carex extensa	1.19	*1 6*	2 47	*1.9*	7.18	*2 4*	3 68	*1 0*	10 96	*2 4*
Juncus gerardii	1.39	*1.9*	4 04	*3.0*	11.20	*3.8*	7 33	*2 0*	4.33	*0 9*
Puccinellia maritima	1.81	*2 5*	3.21	*2 3*	3.13	*1 1*	3 70	*1.0*	4 76	*1.0*
Armeria maritima	0.27		0.61		0.05		+		0 07	
Glaux maritima	+		0.04		0.19		0 02		0 20	
Spergularia media	0.04		0.02		0.14		0 06		0 34	
Salicornia europaea	0.06		0.12		0.26		0.30		0.46	
Suaeda maritima	0.01		0 01		0.03		0 01		0 01	
Cochlearia anglica	0.11		0.26		0.63		0 06		0 03	
Halimione portulacoides	0.14		0.04		0.02		0.52		1.11	
Parapholis strigosa							0 09		+	
Artemisia maritima										
Atriplex hastata					+					
Leontodon autumnalis					0 06					
Not det			0.56		+				0 01	

1969												1970						
Sep.9th	Oct.7th	Average	Apr.21th	May 20th	June 17th	July 15th	Aug.12th	Sep.9th	Oct.7th	Average	May 19th	June 16th	July 15th	Aug.12th	Sep.7th	Oct.5th	Average	
g/m² %	g/m² %	g/m² %	g/m²	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	
521.61	365.75	392.48	245.65	349.78	495.12	582.39	647.46	514.12	489.62	513.08	393.60	579.36	604.58	629.63	675.65	472.22	559.17	
197.38 *37.8*	288.15 *78.8*	143.15 *36.5*		244.26 *69.8*	203.34 *41.0*	185.72 *31.9*	259.94 *40.2*	305.65 *59.4*	371.47 *75.9*	261.73 *51.0*	206.05 *51.4*	232.38 *40.1*	154.26 *25.6*	177.62 *28.2*	252.01 *37.3*	283.17 *60.0*	217.58 *38.9*	
324.23 *62.2*	77.60 *21.2*	249.30 *63.5*		105.52 *30.2*	291.78 *59.0*	396.67 *68.1*	387.51 *59.8*	208.47 *40.6*	118.14 *24.1*	251.35 *49.0*	187.55 *48.6*	346.98 *59.9*	450.32 *74.4*	452.01 *71.8*	423.64 *62.7*	189.05 *40.0*	341.59 *61.1*	
210.39 *64.9*	40.88 *52.7*	163.60 *65.7*		62.66 *59.4*	160.57 *55.0*	242.14 *61.0*	246.24 *63.5*	103.22 *49.5*	51.98 *44.0*	144.47 *57.6*	123.67 *65.9*	175.78 *50.7*	225.72 *50.1*	236.87 *52.4*	252.69 *59.6*	118.69 *62.8*	188.90 *55.2*	
77.54 *23.9*	12.76 *16.4*	54.88 *22.0*		20.41 *19.3*	86.25 *29.6*	94.47 *23.8*	93.17 *24.0*	51.51 *24.7*	33.36 *28.2*	63.20 *25.2*	44.40 *23.7*	126.82 *36.5*	164.75 *36.6*	153.12 *33.9*	108.17 *25.5*	28.80 *15.2*	104.34 *30.5*	
7.53 *2.3*	3.34 *4.3*	6.75 *2.7*		4.43 *4.2*	7.54 *2.6*	15.50 *3.9*	10.60 *2.7*	5.52 *2.6*	1.32 *1.1*	7.49 *3.0*	6.22 *3.3*	17.50 *5.0*	16.66 *3.7*	20.08 *4.4*	13.99 *3.3*	5.24 *2.8*	13.28 *3.9*	
6.65 *2.1*	4.69 *6.0*	4.46 *1.8*		2.89 *2.7*	6.61 *2.3*	11.00 *2.8*	8.81 *2.3*	15.66 *7.5*	10.66 *9.0*	9.27 *3.7*	3.11 *1.7*	5.74 *1.7*	6.77 *1.5*	14.73 *3.3*	7.23 *1.7*	7.18 *3.7*	7.46 *2.2*	
3.69 *1.1*	5.86 *7.6*	4.51 *1.8*		1.77 *1.7*	5.40 *1.9*	5.90 *1.5*	5.77 *1.5*	6.86 *3.3*	8.19 *6.9*	5.65 *2.3*	2.16 *1.2*	4.64 *1.3*	4.74 *1.1*	5.35 *1.2*	8.04 *1.9*	6.42 *3.4*	5.23 *1.5*	
11.38 *3.5*	4.11 *5.3*	5.85 *2.3*		2.55 *2.4*	4.09 *1.4*	2.66 *0.7*	9.52 *2.5*	14.94 *7.2*	3.84 *3.3*	6.27 *2.5*	2.01 *1.1*	2.72 *0.8*	3.84 *0.9*	2.96 *0.7*	2.70 *0.6*	4.44 *2.3*	3.11 *0.9*	
2.16 *0.7*	0.85 *1.1*	4.47 *1.8*		6.93 *6.6*	16.66 *5.7*	17.75 *4.5*	6.70 *1.7*	3.88 *1.9*	1.02 *0.9*	8.82 *3.5*	2.56 *1.4*	6.66 *1.9*	18.16 *4.0*	6.36 *1.4*	4.32 *1.0*	1.09 *0.6*	6.53 *1.9*	
3.84 *1.2*	3.47 *4.5*	3.42 *1.4*		3.43 *3.3*	2.31 *0.8*	2.97 *0.7*	4.14 *1.1*	3.46 *1.7*	2.49 *2.1*	3.13 *1.2*	2.72 *1.5*	4.34 *1.3*	4.56 *1.0*	5.16 *1.1*	6.89 *1.6*	5.81 *3.1*	4.91 *1.4*	
0.12	0.11	0.18		0.02	0.50	0.28	0.10	0.62	1.67 *1.4*	0.53	0.08	0.06	0.05	1.70	4.59 *1.1*	1.23 *0.7*	1.29	
0.24	0.09	0.09			0.08		0.10	0.20	0.04	0.07	0.29	0.29	0.23	0.44	0.47	0.47	0.37	
0.06	0.18	0.11		0.07	0.09	0.05	0.03	0.08	0.13	0.08	0.08	0.17	0.22	0.25	0.27	0.09	0.18	
0.51	0.46	0.31		0.09	0.50	0.86	1.61	1.22 *0.6*	1.58 *1.3*	0.98	0.32	1.33	3.66 *0.8*	3.34 *0.7*	9.26 *2.2*	7.22 *3.8*	4.19 *1.2*	
0.04		0.02		+	0.01	0.06	0.10	0.24	0.02	0.07	0.04	0.23	0.49	0.82	1.55	1.46 *0.8*	0.77	
0.03	0.09	0.17		0.16	0.39	0.03	0.02	0.14	0.14	0.15	+	0.12	0.18	0.06	0.54	0.42	0.22	
0.04	0.69 *0.9*	0.37		0.13	0.71	2.35 *0.6*	0.31	0.92	1.71	1.02	0.04	0.46	0.13	0.44	2.64	+	0.62	
		0.01			0.05	0.64	0.29			0.16			+				+	
					+					+	+	+	+	+			+	
	+	+			+	+				+	+	+	0.13	0.25	0.27	0.33	0.16	
		0.01																
		0.08																

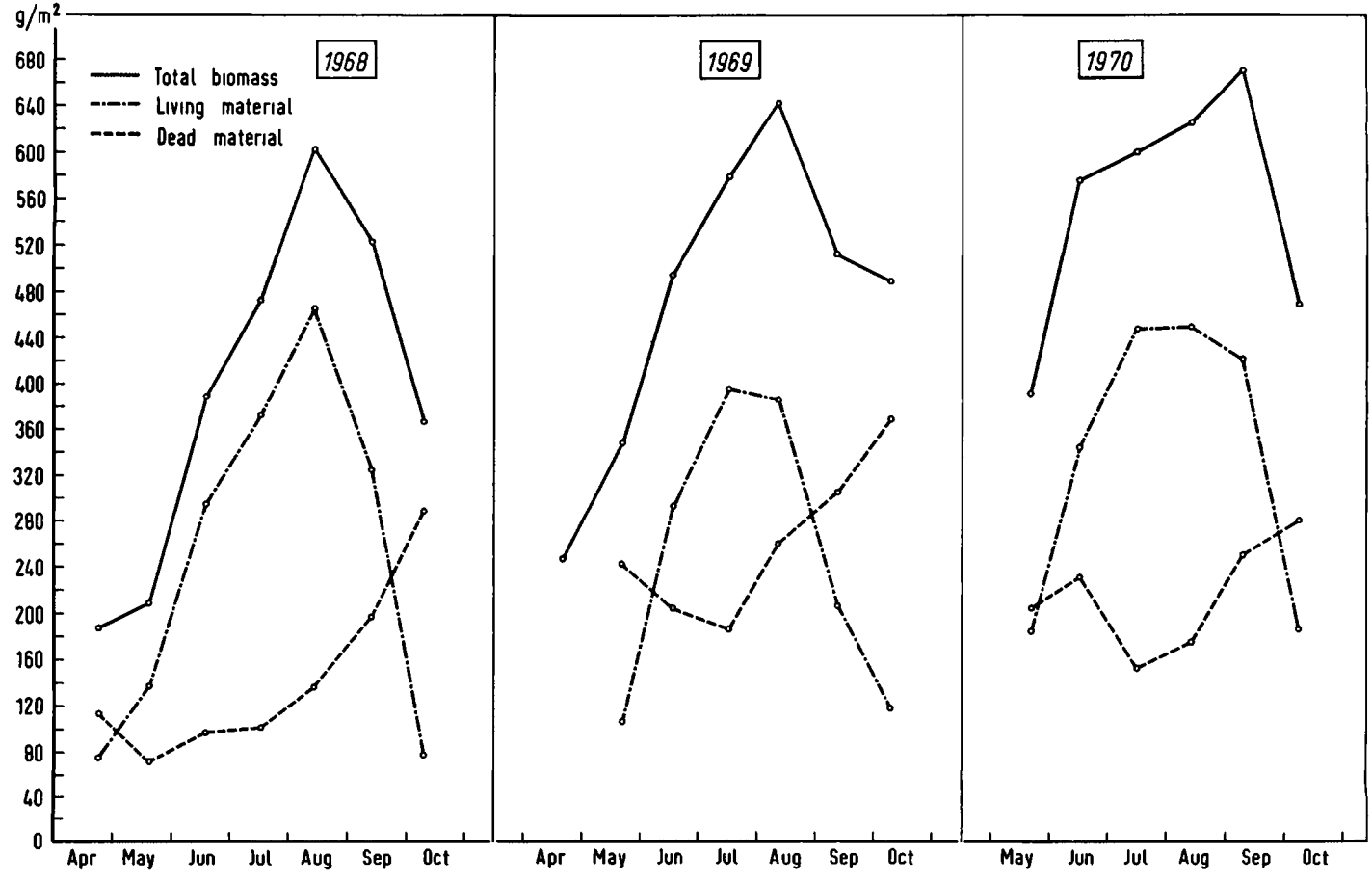

Fig. 11. Changes in standing crop of above-ground material in *Plantagini-Limonietum*, from 1968 to 1970 inclusive

It is difficult to establish how much the dead material still increases after October. The living material certainly still decreases as a result of mortality, but material is also removed by flood-water.

The separation of recent dead material from that of previous years was less difficult than in the JC samples. Table 15 gives the found values in g/m^2.

TABLE 15
Changes in biomass of the dead material in *Plantagini-Limonietum*
(Values in g/m^2)

1970	May 19th	June 16th	July 15th	Aug. 12th	Sep. 7th	Oct. 5th
dead material:						
total	206	232	154	178	252	283
old	200	213	122	107	68	40
newly-formed	6	19	32	71	184	243

As may be expected, the old material decreases during the season, especially in June-July, while much newly-formed, dead plant parts are added from July onwards. Mortality is limited until July, and then increases rapidly. The maximum increase takes place during August-September (113 g/m^2) and in September-October (59 g/m^2). Decomposition of this newly-formed dead material, can however take place at the same time during these periods. This explains the fact, that the rise in the amount of dead material is often not proportional to the sometimes large decrease in green material at the end of the season (see fig. 11).

Living material

There is an increase in living material from April onwards until maximum values are reached in July-August (see table 14 and fig. 11), during the period of optimum development (flowering and fruit setting). In 1968 the maximum (466 g/m^2) is only of short duration; in 1969 the maximum continued; in July and August the biomasses are about the same (397 g/m^2 and 387 g/m^2 resp.), while there is also a lot of living material present in September of that year. From August onwards there is a decrease in the living biomass. In October the amount of living material is about the same as in April or May.

The rate of decrease after August is strongly dependent upon weather and site conditions. For example, during the period August-September 1969 there were many floods and a lot of rain; this resulted in a strong decrease in living material (see fig. 11). The period of August-September 1970 on the other hand was dry and sunny, and there was only a small decrease in green parts. In the September-October period precipitation was again great and inundations were frequent; the decrease in living material was greatest during this last period.

After the October harvest, the amount of living material will fall even more due to flooding and frost. The amount of living material present during the winter could not be established.

Just as the curves for the development of the dead and living material are very similar to each other, the curves for the total biomass (dead and living) are also most identical.

The total standing crop gives little information about the actual growth, as can be seen e.g. in 1968, in which the greatest maximum value for the living biomass is found, but the lowest maximum value for the total biomass.

There appears to be a slight rise in the amount of total biomass during the three years of research. This is, however, more the result of a difference in the amounts of dead material than of a difference in living material.

Floristic composition

The species composition of the PL samples is rather constant. On average there were always 16 species present, 8 of which each constitute less than 0.5% of the total, living biomass (see table 14).

The dominant species, *Plantago maritima* and *Limonium vulgare*, constitute 80%-90% of the living biomass; *Pl. maritima* is the most important of the two; its proportion in the living biomass varies from 45%-80%. The other important species, such as *Triglochin maritima, Aster tripolium, Puccinellia maritima, Festuca rubra f. litoralis, Carex extensa* and *Juncus gerardii*, always contribute less than 10%. In October the proportion of *Pl. maritima* and *L. vulgare* falls, as a result of the rapid dying off of these plants, while *F. rubra, C. extensa, Pucc. maritima* and *J. gerardii* remain green for a longer time. Fig.12 shows the curves of the monthly biomasses found for *Pl. maritima, L. vulgare* and *Tr. maritima*. The large proportion of *Pl. maritima* and *L. vulgare* in the total living production, accounts for the similarity of the curves for these species with those for the total living material (cf. fig.11 with fig.12). In 1968 *Pl. maritima* attained optimum development; there was very profuse flowering and the biomass reached a maximum of 330 g/m^2 in August. The maximum values in 1969 and 1970 were much lower, 246 and 253 g/m^2 respectively. In 1969 *Pl. maritima* flowered less than in 1968, and during flowering and fruit setting (July-August) there was high mortality of the leaves. In July and August the same amounts of material were found. In 1970 *Plantago* flowered only slightly and the mortality of the leaves in summer was low. The weather conditions in late summer were favourable. A peak in standing crop was reached in September. See also table 16 in which the differences in biomass of the leaves and flowering parts are given for *Plantago*.

The development of *L. vulgare* is constant in the three years of investigations. Maximum standing crops are found in July-August. In 1968 and 1969 the

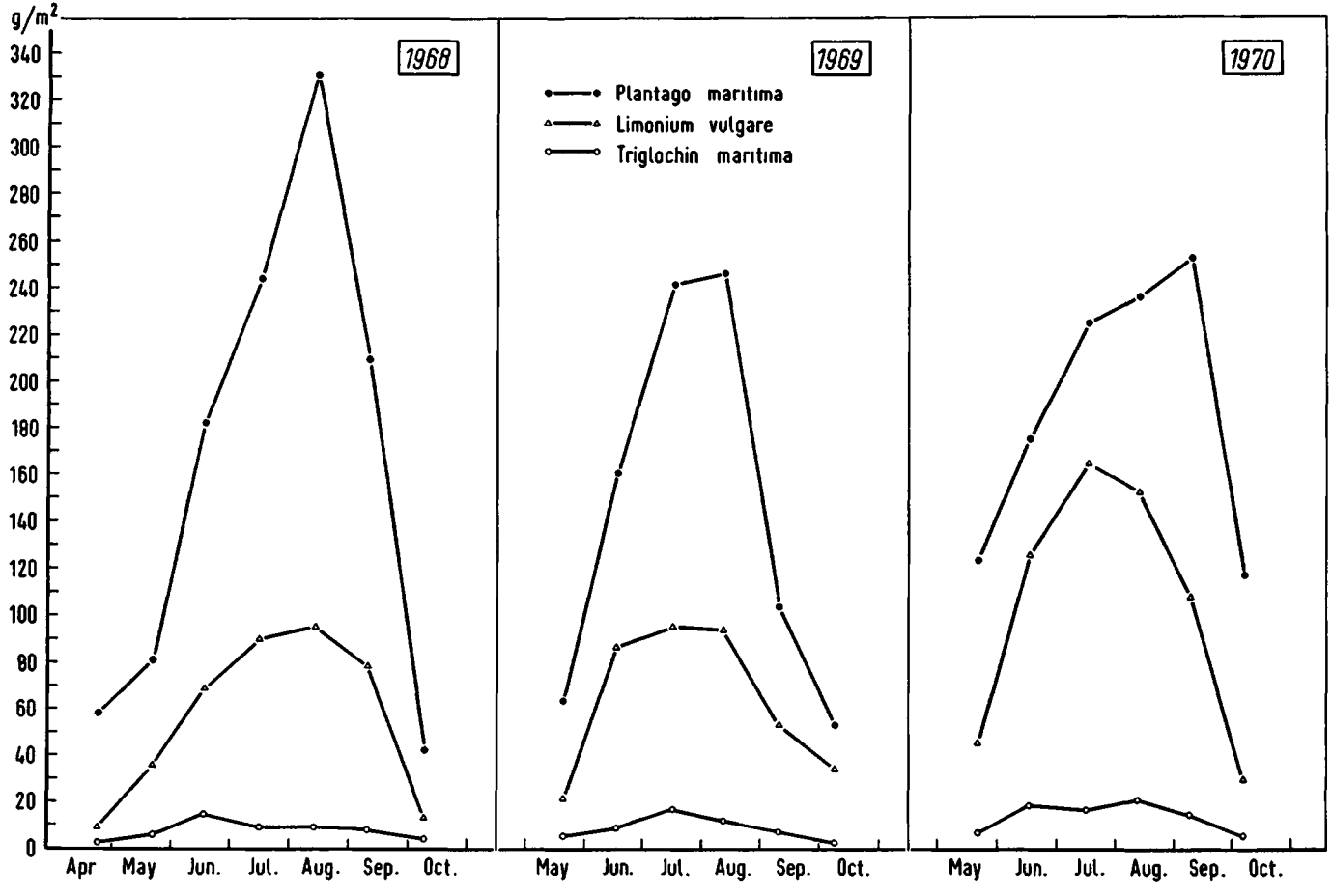

Fig. 12. Changes in standing crop of important species in *Plantagini-Limonietum*, from 1968 to 1970 inclusive

TABLE 16
Changes in biomass of the leaves and flowering stalks in *Plantago maritima*
(Values in g/m^2)

1970	May 19th	June 16th	July 15th	Aug.12th	Sep.7th	Oct.5th
total biomass	124	176	225	237	253	119
leaves	124	176	224	230	241	
flowering stalks			1	7	12	

maximum is 94 g/m^2. There is much more *Limonium* in 1970; the maximum standing crop in July is then 165 g/m^2. This increase is presumably only a result of very profuse flowering; in August 1968 an average of 44 flowering stalks were counted per m^2, in 1970 this amounted to 72 (see table 17). In May of those years the amount of biomass was still about the same (34 g/m^2 in 1968; 44 g/m^2 in 1970). Table 17 gives the biomasses of leaves and flowering stalks of *L. vulgare* separately.

TABLE 17
Changes in biomass of the leaves and flowering stalks in *Limonium vulgare*
(Values in g/m^2)

1970	May 19th	June 16th	July 15th	Aug.12th	Sep.7th	Oct.5th
total biomass	44	127	165	153	108	29
leaves	44	127	148	111	71	26
flowering stalks			17	42	37	3
number of flowering stalks/m^2			60	72	60	12

This table shows that the maximum in leaf biomass (in July) is reached before that of the flowering stalks (August-September). While the flowering parts are still increasing in weight (flowers, fruit setting), there is a noticeable mortality of the leaves. In August-September the leaf biomass decreases still more, while the standing crop of flowering stalks is still the same; the number of flowering stalks is, however, somewhat reduced. In the following period they also rapidly die off. In October there are only 12 living flowering stalks per m^2 and 48 dead ones. The flowering parts were considered dead when no more green parts could be seen. In October 1970 the biomass of *Limonium* is almost the same as that of October 1969.

For *Tr. maritima* a shift in the maximum to a later date is noticed (see fig.12); at the same time this maximum increases (14 g/m^2 in June 1968; 16 g/m^2 in July 1969; 20 g/m^2 in August 1970). *Tr. maritima* flowers early, but grows throughout the whole season. The amount of *Tr. maritima* is small compared with that of *Pl. maritima* and *L. vulgare*. Differences in yield could then easily

be a result of measuring errors. Nevertheless the changes in biomass reflect the development in the field. The proportion of *Tr. maritima* in the total, living biomass is greatest in May or June (4%-5%). In 1968 much insect damage of the plants was noticed.

No development curves were made for the other species. In the frequently appearing species e.g. *Aster tripolium, Salicornia europaea, Suaeda maritima*, etc., the maximum in standing crop coincides with the phenophase of flowering and fructification. *Aster tripolium* usually attains maximum development in the second half of August. In 1970, however, there was a great deal of leaf mortality and damage by animals to the plants during the flowering period. The maximum biomass is reached in the beginning of August of that year. The frequent occurrence of *Sal. europaea* is noticeable in 1970. The maximum standing crop in September of that year was 20 times greater than in September 1968 and the proportion in the total, living biomass was 4%. Much more *Salicornia* was also found in the surrounding areas in 1970 than in the previous years.

The increase in standing crop of a few species from August-September is not evident in the total, living biomass, as it is overpowered by the sharp decrease in weight of the dominant species *Pl. maritima* and *L. vulgare*.

TABLE 18

Frequency of occurrence of the species (in percentages) in the total number of cut samples (of 0.125 m^2) in *Plantagini-Limonietum*

	1968	1969	1970
Total number of cut samples	105	74	66
Plantago maritima	100	100	100
Limonium vulgare	100	100	100
Triglochin maritima	99	100	100
Aster tripolium	98	99	100
Puccinellia maritima	95	84	77
Juncus gerardii	40	56	36
Carex extensa	41	40	47
Salicornia europaea	86	90	97
Suaeda maritima	35	43	85
Spergularia media	32	38	45
Armeria maritima	13	20	20
Cochlearia anglica	60	54	41
Festuca rubra f. litoralis	79	85	92
Halimione portulacoides	39	43	44
Glaux maritima	12	9	20
Parapholis strigosa	7	19	3
Atriplex hastata	2	4	32
Artemisia maritima	–	1	21

Table 18 gives the frequency of occurrence of the species in the samples of 0.125 m^2 in the various years. The performance of annual species fluctuates greatly, e.g. *Suaeda maritima, Parapholis strigosa, Cochlearia anglica* and *Atriplex hastata*. The latter, a nitrophilous species, usually occurring frequently on the flood-mark, is present in a great deal in 1970 due to inundations of PL at the end of April. A lot of flood-mark material was deposited at that time against the cages. Although this material was removed, *Atriplex* seeds, which were carried along the floods remained behind and germinated. The plants, however, did not reach optimum development. *Pucc. maritima* occurs somewhat less often in the samples of 1970 than in those of 1968; *F. rubra* somewhat more often. The increase in *Artemisia maritima* is also striking (see also discussion). Attention should be paid to the fact that an increase or decrease in the frequency in occurrence of a species does not necessarily coincide with an increase or decrease in weight (cf. e.g. the frequency and biomass of *C. extensa* in tables 18 and 14 resp.).

PUCCINELLIETUM MARITIMAE – Enclosures

The vegetation of the cattle-grazed PM area develops later than that of JC and PL and moreover, due to the fact that the site was very wet at the end of April, the first samples could only be taken during the first or second week in May. The vegetation cages were placed on different plots each year. The changes in standing crop were thus determined annually from a vegetation which had only been excluded from the effects of grazing for one season. The samples taken from outside the cages were used as comparisons. In 1967 harvesting was carried out only 5 times during the growing season, in the other years 7 times. The harvest of August 1969 and July 1970 took place under very bad weather conditions. In May 1970, before the beginning of grazing and shortly after the cages had been re-placed, samples were taken from the plots where the cages had stood in 1969. These samples of 1/16 m^2 were cut and the material divided only into dead and living parts.

Dead material

The development of the dead material is very similar over the 4 years of investigations (see fig.13). The minimum amount of dead biomass is found in spring. In 1967, 1968 and 1969 the biomass amounted to 25 g/m^2 in May and in the same month in 1970 this was 66 g/m^2 (see table 19). The dead material consists mainly of old, woody stalks of *Salicornia europaea*, and also of leaf remains of *Limonium vulgare* and *Puccinellia maritima*. The much greater amount of dead material in May 1970, compared with the other years, is partly due to the large production of material in 1969 (cf. fig.15 for PM-A), and partly to the limited decomposition in the spring of 1970 (cf. JC and PL).

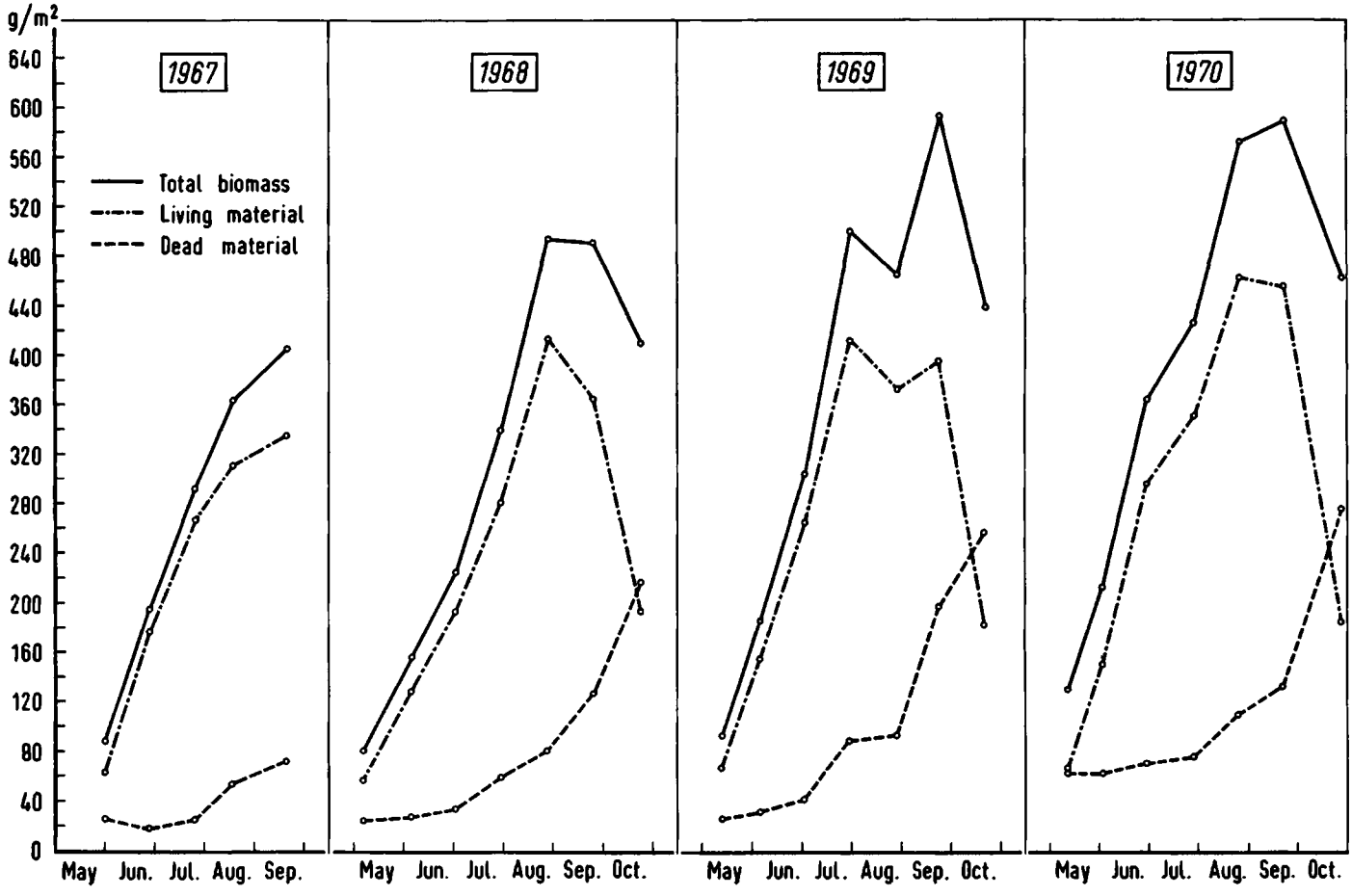

Fig. 13. Changes in standing crop of above-ground material in ungrazed (in enclosures) *Puccinellietum maritimae*, from 1967 to 1970 inclusive

TABLE 19

Changes in standing crop of dead material, living material and total vegetation in g/m^2 and in percentage of weight of total biomass, in ungrazed (in enclosures) and grazed *Puccinellietum maritimae*

Also the portion of the various species in g/m^2 and in percentage of weight of the living material.

Percentages less than 0 5 are not given

PUCCINELLIETUM MARITIMAE (enclosures)

Year	1967									
date	May 30th		June 26th		July 24th		Aug 17th		Sep.19th	
	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%
Total biomass	87 94		195 12		291.51		362 63		406 73	
Dead material	25.26	*28.7*	17.96	*9.2*	25.26	*8.7*	53 05	*14.6*	71.69	*17 6*
Living material	62.68	*71 3*	177.16	*90 8*	266.25	*91.3*	309.58	*85.4*	335.04	*82 4*
Species										
Puccinellia maritima	48.81	*77 9*	126.91	*71.6*	175 13	*65.8*	195 04	*63.0*	183 54	*54 8*
Plantago maritima	5.63	*9.0*	28.14	*15.9*	41.77	*15.7*	37.17	*12 0*	43.12	*12 9*
Salicornia europaea	0.74	*1.2*	5.22	*2.9*	22.77	*8.6*	48.98	*15 8*	77 88	*23 2*
Triglochin maritima	2.10	*3.4*	4.26	*2.4*	12.52	*4.7*	7 96	*2 6*	11	*1.8*
Spergularia media	1.32	*2.1*	2.40	*1.4*	4.58	*1.7*	6 73	*2.2*	6 23	*1.9*
Suaeda maritima	0 02		0.18		0.61		3.03	*1.0*	6 72	*2.0*
Aster tripolium	0.39	*0.6*	2.95	*1.7*	4.14	*1.6*	3.33	*1.1*	5.93	*1 8*
Limonium vulgare	0.12		0.93	*0.5*	1.64	*0.6*	0.33		1 39	
Glaux maritima	0.67	*1.1*	3.32	*1.9*	2 31	*0.9*	6.08	*2.0*	2.78	*0.8*
Spartina townsendii	1.52	*2.4*	1.63	*0.9*	0.79					
Juncus gerardii	1.28	*2 0*	0.17				0 57		1.30	
Cochlearia anglica	0.04									
Halimione portulacoides			1.04	*0.6*			0 29		0.02	
Halimione pedunculata										
Carex extensa										
Scirpus rufus					+					
Not det.	0.02									

PUCCINELLIETUM MARITIMAE (grazed)

Year	1967									
date	June 1st		June 27th		July 24/26th		Aug 18th		Sep.18th	
	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%	g/m^2	%
Total biomass	101.29		141.36		230.97		248.16		303 82	
Dead material	31.41	*31.0*	14.54	*10.3*	23.47	*10.2*	42.18	*17.0*	75 35	*24.8*
Living material	69 88	*69.0*	126.82	*89.7*	207.50	*89.8*	205.98	*83.0*	228.47	*75.2*
Species										
Puccinellia maritima	49.03	*70.2*	102.31	*80.7*	137.74	*66 4*	129.87	*63.0*	152.12	*66.6*
Plantago maritima	10.52	*15.1*	6.39	*5.0*	31.98	*15.4*	27.41	*13.3*	4.93	*2.2*
Salicornia europaea	0.90	*1.3*	5.92	*4.7*	17.31	*8.3*	29 80	*14.5*	61.85	*27.1*
Triglochin maritima	1.68	*2.4*	4.53	*3.6*	9.73	*4.7*	7 88	*3.8*	2.10	*0.9*
Spergularia media	1.50	*2.1*	4.73	*3.7*	4.18	*2.0*	5.16	*2.5*	5 46	*2.4*
Suaeda maritima	0.03		0.18		0.60		1.24	*0 6*	0.73	
Aster tripolium	1.33	*1.9*	0.49		1.88	*0.9*	2.09	*1.0*	1.01	
Limonium vulgare	3.03	*4.3*	2.25	*1.8*	1.24	*0.6*	0.14		0.20	
Glaux maritima					0.51		1.01	*0.5*	0.03	
Spartina townsendii	1.81	*2.6*					0.06			
Juncus gerardii			0.01		2.31	*1.1*	1.18	*0.6*	0.04	
Cochlearia anglica	0.05									
Halimione portulacoides			0.01		0.02		0.14			
Halimione pedunculata										

There is only a slight rise in dead material until August; then the amount increases rapidly when many plants die off after flowering and fruit setting. The largest increase is usually found in the period September-October. In 1969 this was in the August-September period, presumably due to rain and flooding at the end of August. Maximum amounts of dead biomass are present in October and vary from 217 g/m^2 (1968) to 277 g/m^2 (1970). Apart from the autumn the amount of dead material is always less than the amount of living material. The proportion of dead material in the total biomass is the smallest in July (8%-17.8%); in October this amounts to ± 60%. No distinction was made between old, dead material and recent dead material, as was the case in JC and PL. In May it is chiefly the old, dead material that is present. This will decrease during the season as shown in JC and PL; so the dead material in October is probably almost exclusively newly-formed.

Living material

Just as for the dead material, the curves showing the development of the living material are almost identical (see fig.13).

In spring the amount of green material is small; the values vary from 56 g/m^2 (May 6th, 1968) to 67 g/m^2 (May 11th, 1970). In 1967 there are only a few green parts even at the end of May (63 g/m^2). This small amount in 1967 is due to the development in the previous year. In 1966 there was a great deal of rain (> 1000 mm), also during the growing season, and as a result of this many plants suffered from grazing (i.e. trampling).

From May onwards the living material increases almost linearly until the maximum value is reached. This occurs in July (413 g/m^2 in 1969), in August (413 g/m^2 and 463 g/m^2 in 1968 and 1970 resp.) or in September (335 g/m^2 in 1967). The peak sometimes continues for a short period. The fall in living material in August 1969, followed by an increase, is noteworthy. During the week of harvesting, there was a great deal of rain and often high floods. The mortality of the green material was high. This is not reflected in an increase of dead material, presumably partly due to a sampling error and partly due to rapid decomposition of the material or to the removal of material by the flood-water. In September the vegetation recovers again (favourable weather conditions). In the second half of September and in October the vegetation decreases rapidly. In November there is usually no more living material present here. As a result of seed loss and rapid decomposition of the succulent plant parts (e.g. of *Pl. maritima*, *Sal. europaea* and *Su. maritima*) the decrease in living material in autumn is sometimes much greater than the increase in dead material.

The curves for the total biomass run almost parallel with those for the living material. Maximum values are reached in September. After the peak there is no

1968									1969								1970							
Average	May 6th	June 4th	July 1st	July 29th	Aug.27th	Sep.24th	Oct.23rd	Average	May 12th	June 4th	July 2nd	July 29th	Aug.27th	Sep.23rd	Oct.20th	Average	May 11th	June 1st	June 29th	July 27th	Aug.24th	Sep.21st	Oct.26th	Average
g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %
268.79	80.22	156.69	225.62	339.41	493.88	491.60	410.94	314.05	92.45	186.49	304.63	501.36	466.14	593.71	439.63	369.20	129.92	213.46	366.07	428.58	573.85	589.93	462.62	394.92
38.64 *14.4*	24.51 *30.6*	27.15 *17.3*	33.41 *14.8*	58.47 *17.2*	80.00 *16.2*	126.13 *25.7*	217.54 *52.9*	81.03 *25.8*	26.70 *28.9*	31.17 *16.7*	40.24 *13.2*	88.13 *17.6*	92.96 *20.0*	197.34 *33.2*	256.90 *58.4*	104.78 *28.4*	63.21 *48.7*	62.06 *29.1*	69.76 *19.1*	76.20 *17.8*	110.06 *19.2*	133.20 *22.6*	277.18 *59.9*	113.10 *28.6*
230.15 *85.6*	55.71 *69.4*	129.54 *82.7*	192.21 *85.2*	280.94 *82.8*	413.88 *83.8*	365.47 *74.3*	193.40 *47.1*	233.02 *74.2*	65.75 *71.1*	155.32 *83.3*	264.39 *86.8*	413.23 *82.4*	373.18 *80.0*	396.37 *66.8*	182.74 *41.6*	264.42 *71.6*	66.71 *51.3*	151.40 *70.9*	296.31 *80.9*	352.38 *82.2*	463.79 *80.8*	456.73 *77.4*	185.44 *40.1*	281.82 *71.4*
145.89 *63.4*	32.89 *59.0*	75.89 *58.6*	123.62 *64.3*	129.67 *46.2*	201.71 *48.7*	166.22 *45.5*	169.39 *87.6*	128.48 *55.1*	36.22 *55.1*	81.62 *52.5*	152.18 *57.6*	194.85 *47.2*	160.85 *43.1*	152.66 *38.5*	123.17 *67.4*	128.79 *48.8*	45.90 *68.8*	93.38 *61.7*	154.76 *52.2*	163.91 *46.5*	187.59 *40.4*	173.34 *38.0*	139.70 *75.3*	136.94 *48.6*
31.17 *13.6*	14.90 *26.7*	24.61 *19.0*	16.53 *8.6*	62.28 *22.2*	53.27 *12.9*	35.31 *9.7*	6.84 *3.5*	30.53 *13.1*	18.20 *27.7*	42.81 *27.6*	49.26 *18.6*	89.94 *21.8*	69.18 *18.5*	49.73 *12.5*	28.58 *15.6*	49.67 *18.8*	14.82 *22.2*	18.49 *12.2*	42.60 *14.4*	38.72 *11.0*	55.85 *12.0*	25.75 *5.6*	11 60 *6.3*	29.69 *10.5*
31.12 *13.5*	1.87 *3.4*	7.66 *5.9*	23.63 *12.3*	41.78 *14.9*	107.38 *25.9*	109.37 *29.9*	2.29 *1.2*	42.00 *18.0*	1.53 *2.3*	4.20 *2.7*	22.10 *8.4*	44.48 *10.8*	63.39 *17.0*	83.10 *21.0*	11.94 *6.5*	32.96 *12.5*	1.63 *2.4*	14.04 *9.3*	41.42 *14.0*	81.79 *23.2*	165.22 *35.6*	217.34 *47.6*	17.82 *9.6*	77.04 *27.3*
6.59 *2.9*	1.83 *3.3*	5.30 *4.1*	11.51 *6.0*	14.83 *5.3*	4.61 *1.1*	2.46 *0.7*	3.69 *1.9*	6.32 *2.7*	3.98 *6.1*	11.06 *7.1*	14.94 *5.7*	12.65 *3.1*	14.61 *3.9*	4.20 *1.1*	0.36	8.83 *3.3*	1.10 *1.6*	6.16 *4.1*	22.30 *7.5*	28.25 *8.0*	11.53 *2.5*	3.89 *0.9*	0.18	10.49 *3.7*
4.25 *1.8*	1.92 *3.6*	3.40 *2.6*	6.52 *3.4*	13.83 *4.9*	14.67 *3.5*	9.41 *2.6*	4.69 *2.4*	7.78 *3.4*	1.58 *2.4*	3.22 *2.1*	7.06 *2.7*	14.47 *3.5*	7.33 *2.0*	8.47 *2.1*	9.43 *5.2*	7.37 *2.8*	0.96 *1.4*	3.78 *2.5*	9.30 *3.1*	6.91 *2.0*	8.18 *1.8*	7.01 *1.5*	4.49 *2.4*	5.80 *2.1*
2.11 *0.9*	0.08	0.25	1.05 *0.5*	1.57 *0.6*	10.13 *2.4*	13.67 *3.7*	1.96 *1.0*	4.10 *1.8*	0.13	0.34	2.74 *1.0*	6.44 *1.6*	9.20 *2.5*	22.28 *5.6*	0.42	5.94 *2.3*	0.30	0.87 *0.6*	4.42 *1.5*	6.58 *1.9*	14.51 *3.1*	13.62 *3.0*	1.91 *1.0*	6.03 *2.1*
3.35 *1.5*	0.90 *1.6*	.80 *2.1*	3.70 *1.9*	2.68 *1.0*	11.14 *2.7*	14.24 *3.9*	3.04 *1.6*	5.50 *2.4*	3.12 *4.7*	5.50 *3.5*	3.56 *1.3*	14.16 *3.4*	25.57 *6.9*	40.61 *10.2*	5.13 *2.8*	13.95 *5.3*	1.03 *1.5*	3.89 *2.6*	1.86 *0.6*	0.82	5.13 *1.1*	7.30 *1.6*	1.02 *0.6*	3.01 *1.1*
0.88	0.01	.72 *0.6*	1.03 *0.5*	5.58 *2.0*	2.44 *0.6*	2.46 *0.7*	0.03	1.75 *0.8*	0.80 *1.2*	3.62 *2.3*	5.29 *2.0*	19.27 *4.7*	11.14 *3.0*	18.34 *4.6*	3.41 *1.9*	8.81 *3.3*	0.63 *0.9*	7.93 *5.2*	9.67 *3.3*	25.17 *7.1*	11.49 *2.5*	3.32 *0.7*	0.57	8.40 *3.0*
3.03 *1.3*	+	+	+	0.40	6.13 *1.5*	2.20 *0.6*	0.11	1.26 *0.5*	0.33 *0.5*	2.90 *1.9*	3.84 *1.5*	3.67 *0.9*	4.29 *1.1*	1.41	0.08	2.36 *0.9*	0.14	0.01	1.38 *0.5*	0.23	3.33 *0.7*	1.10		0.88
0.79	1.26 *2.3*	.29 *1.8*		0.82	2.41 *0.6*	3.85 *1.1*	0.48	1.59 *0.7*	+	0.05	3.38 *1.3*			15.55 *3.9*	0.22	2.74 *1.0*	0.14	2.70 *1.8*	8.45 *2.9*		0.68	4.05 *0.9*	8.15 *4.4*	3.45 *1.2*
0.66		.45 *5.0*	3.38 *1.8*	7.50 *2.7*		6.13 *1.7*	0.87	3.48 *1.5*				12.96 *3.1*	7.47 *2.0*	+		2.92 *1.1*	0.06					0.02		0.01
0.01		+			+	0.12		0.02	+			+	+			+		0.14						0.02
0.27		+	0.01				0.02	+		+	0.05	0.04	0.07	+		0.02								
		0.10	1.21 *0.6*			0.03		0.19											0.14		0.19			0.05
+																								
+	0.05							0.01																

1968								1969							1970							
Average	May 6th	; ne 4th	July 2nd	July 30th	Aug.27/28th	Sep.25th	Oct.24th	Average	May 12th	June 5th	July 3rd	July 30th		Sep.24th	Oct.21st	Average	May 11th		June 29th	July 28th	Aug.25th	Sep.25th	Oct.27th	Average
g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m²	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %		g/m² %	g/m² %	g/m² %	g/m² %		g/m² %	g/m² %	g/m² %	g/m² %	g/m² %	g/m² %
205.12	80.22	134.81	195.27	286.51	239.29	255.45	120.87	198.59	92.45	160.03	254.24	352.49		393.64	232.61	247.58	129.92		343.09	299.93	359.18	469.76	277.06	313 16
37.39 *18.2*	24.51 *30.6*	27.86 *20.7*	30.14 *15.4*	53.62 *18.7*	50.63 *21.2*	67.07 *26.3*		42.31 *21.3*	26.70 *28.9*	29.72 *18.6*	41.82 *16.4*	92.66 *26.3*		142.58 *36.2*	133.26 *56.1*	77.79 *31.4*	63.21 *48.7*		69.58 *20.3*	52.78 *17.6*	75.89 *21.1*	127.64 *27.2*	169.03 *61.0*	93.02 *29.7*
167.73 *81.8*	55.71 *69.4*	106.95 *79.3*	165.13 *84.6*	232.89 *81.3*	188.66 *78.8*	188.38 *73.7*		156.28 *78.7*	65.75 *71.1*	130.31 *81.4*	212.42 *83.6*	259.83 *73.7*		251.06 *63.8*	99.35 *43.9*	169.79 *68.6*	66.71 *51.3*		273.51 *79.7*	247.15 *82.4*	283.29 *78.9*	342.12 *72.8*	108.03 *39.0*	220.14 *70.3*
114.21 *68.0*	32.89 *59.0*	64.88 *60.7*	105.94 *64.2*	129.19 *55.5*	93.20 *49.4*	86.30 *45.8*		85.40 *54.7*	36.22 *55.1*	83.75 *64.3*	120.60 *56.8*	136.91 *52.7*		124.29 *49.5*	60.02 *61.6*	93.63 *55.1*	45 90 *68.8*		180.62 *66.0*	146.14 *59.1*	132.55 *46.8*	123.45 *36.1*	82.15 *76.0*	118.47 *53.9*
16.25 *9.7*	14.90 *26.7*	22.45 *21.0*	13.53 *8.2*	32.92 *14.1*	20.81 *11.0*	19.14 *10.2*		20.63 *13.2*	18.20 *27.7*	25.29 *19.4*	52.15 *24.6*	57.78 *22.2*		18.54 *7.4*	3.42 *3.5*	29.23 *17.2*	14.82 *22.2*		30.06 *11.0*	19.77 *8.0*	17.72 *6.3*	16.35 *4.8*	2.41 *2.2*	16.86 *7.7*
23.16 *13.8*	1.87 *3.4*	4.53 *4.2*	17.94 *10.9*	37.22 *16.0*	58.07 *30.8*	62.30 *33.1*		30.32 *19.4*	1.53 *2.3*	4.84 *3.7*	10.86 *5.1*	28.46 *11.0*		82.13 *32.7*	16.38 *16.8*	24.03 *14.1*	1.63 *2.4*		34.02 *12.4*	56.06 *22.7*	113.34 *40.0*	159.71 *46.7*	12.12 *11.2*	62.81 *28.6*
5.18 *3.0*	1.83 *3.3*	5.55 *5.2*	6.95 *4.2*	4.40 *1.9*	4.94 *2.6*	3.09 *1.6*		4.46 *2.9*	3.98 *6.1*	3.49 *2.6*	8.06 *3.8*	10.95 *4.2*		0.09	0.44 *0.5*	4.50 *2.6*	1.10 *1.6*		8.98 *3.3*	4.43 *1.8*	2.83 *1.0*	4.86 *1.4*	1.41 *1.3*	3.94 *1.8*
4.21 *2.5*	1.92 *3.6*	3.99 *3.7*	8.66 *5.2*	9.82 *4.2*	4.59 *2.4*	5.70 *3.0*		5.78 *3.7*	1.58 *2.4*	2.91 *2.2*	7.02 *3.3*	8.26 *3.2*		4.77 *1.9*	1.68 *1.7*	4.37 *2.6*	0.96 *1.4*		8.22 *3.0*	11.82 *4.8*	5.64 *2.0*	6.20 *1.8*	2.02 *1.9*	5.81 *2.6*
0.56	0.08	0.11	0.66	1.40 *0.6*	1.30 *0.7*	3.22 *1.7*		1.13 *0.7*	0.13	0.39	1.76 *0.8*	4.46 *1.7*		16.74 *6.7*	0.07	3.93 *2.3*	0.30		6.42 *2.3*	5.15 *2.1*	5.79 *2.0*	6.88 *2.0*	0.63 *0.6*	4.20 *1.9*
1.36 *0.8*	0.90 *1.6*	1.26 *1.2*	2.94 *1.8*	5.17 *2.2*	2.63 *1.4*	5.89 *3.1*		3.13 *2.0*	3.12 *4.7*	4.51 *3.5*	1.24 *0.6*	2.67 *1.0*		2.31 *0.9*	3.15 *3.2*	2.83 *1.7*	1.03 *1.5*		0.58	0.99	1.13	4.04 *1.2*	0.19	1.33 *0.6*
1.37 *0.8*	0.05	1.90 *1.8*	1.28 *0.8*	2.92 *1.2*	1.98 *1.0*	0.98 *0.5*		1.52 *1.0*	0.80 *1.2*	4.27 *3.3*	9.13 *4.3*	6.12 *2.4*		2.04 *0.8*	6.58 *4.9*	4.82 *2.8*	0.63 *0.9*		2.61 *1.0*	2.46 *1.0*	0.98	15.92 *4.7*	2.69 *2.5*	4.22 *1.9*
0.31	+	1.30 *1.2*	0.98 *0.6*	1.38 *0.6*	1.14 *0.6*	1.76 *0.9*		1.09 *0.7*	0.33 *0.5*	0.76 *0.6*	1.08 *0.5*	3.10 *1.2*		0.15		0.90	0.14		0.66	0.33	0.87			0.33
0.37	1.26 *2.3*	0.97 *0.9*	0.10	3.08 *1.3*				0.90 *0.6*	+	0.06	0.54	1.04			7.61 *7.8*	1.54 *1.0*	0.14		1.34 *0.5*		2.44 *0.9*	1.59 *0.5*	4.41 *4.1*	1.65 *0.8*
0.71			6.14 *3.7*	5.39 *2.3*				1.92 *1.2*				+				+	0.06					2.55 *0.7*		0.44
0.01			0.01						+							+								
0.03																						+		+
																						0.57		0.10

decrease to values which correspond with those of the dead material in the following spring, as was the case in JC and PL. Because grazing is discontinued (for one season only), there is an accumulation of material and a new equilibrium must develop between decay, mortality and growth.

In May 1970 226 g/m^2 dead material and 108 g/m^2 living material was found in the plots of 1969. This is much more than was found in the enclosures in 1970. The large amount of dead material acts as a protection for the development of the living material; and moreover there are more young shoots present, because there was no grazing during the previous year. The places where the cages had stood were still visible in the area after three years.

Floristic composition

A total of 19 different taxa were found in PM (see table 19). An average of 11 species was always present in the samples; *Pucc. maritima, Pl. maritima* and *Sal. europaea* together constituted 85%-90% of the total living biomass. Other frequently occurring species are *Tr. maritima, Su. maritima, Spergularia media, A. tripolium* and *L. vulgare*, which may contribute from 1%-10% of the living biomass.

At the beginning of the season mainly *Pucc. maritima* (up to 78%) and *Pl. maritima* (up to 27%) are present. The proportion of these plants decreases during the season, while that of *Salicornia* rises from 1% to a maximum of 47% (September 1970). In October the living material again consists mainly of *Puccinellia*, when due to rain and inundation nearly all the other taxa die off. Fig.14 illustrates the development of a few important species. The maximum value for the standing crop of *Pucc. maritima* is reached in August (except in 1969) and is very constant (195 g/m^2 in 1967; 201 g/m^2 in 1968; 195 g/m^2 in 1969; 188 g/m^2 in 1970).

Salicornia europaea shows much greater fluctuations in standing crop over the years. The maximum is reached in September each year, but in September 1970 almost 3 times as much *Salicornia* is present than in September 1967 (217 g/m^2 and 77 g/m^2 resp.). The amounts of *Salicornia* in May are all about the same (1.53-1.87 g/m^2), except in 1967 (0.74 g/m^2). After germination of the seed at the end of April - beginning of May, not all the seedlings develop completely; the mortality can be high especially in the first weeks after germination (cf. Wiehe, 1935). Consequently there is only a slight increase in biomass in the May-June period. Then the increase is linear until September (see fig.14). Mortality is very low between June and September. After flowering and fruit setting the biomass decreases rapidly as a result of decay and seed loss. In October almost no living plants of *Sal. europaea* are present.

The development of *Pl. maritima* is almost the same each year. The maximum in biomass is usually at the end of July. In 1969 more *Plantago* was present

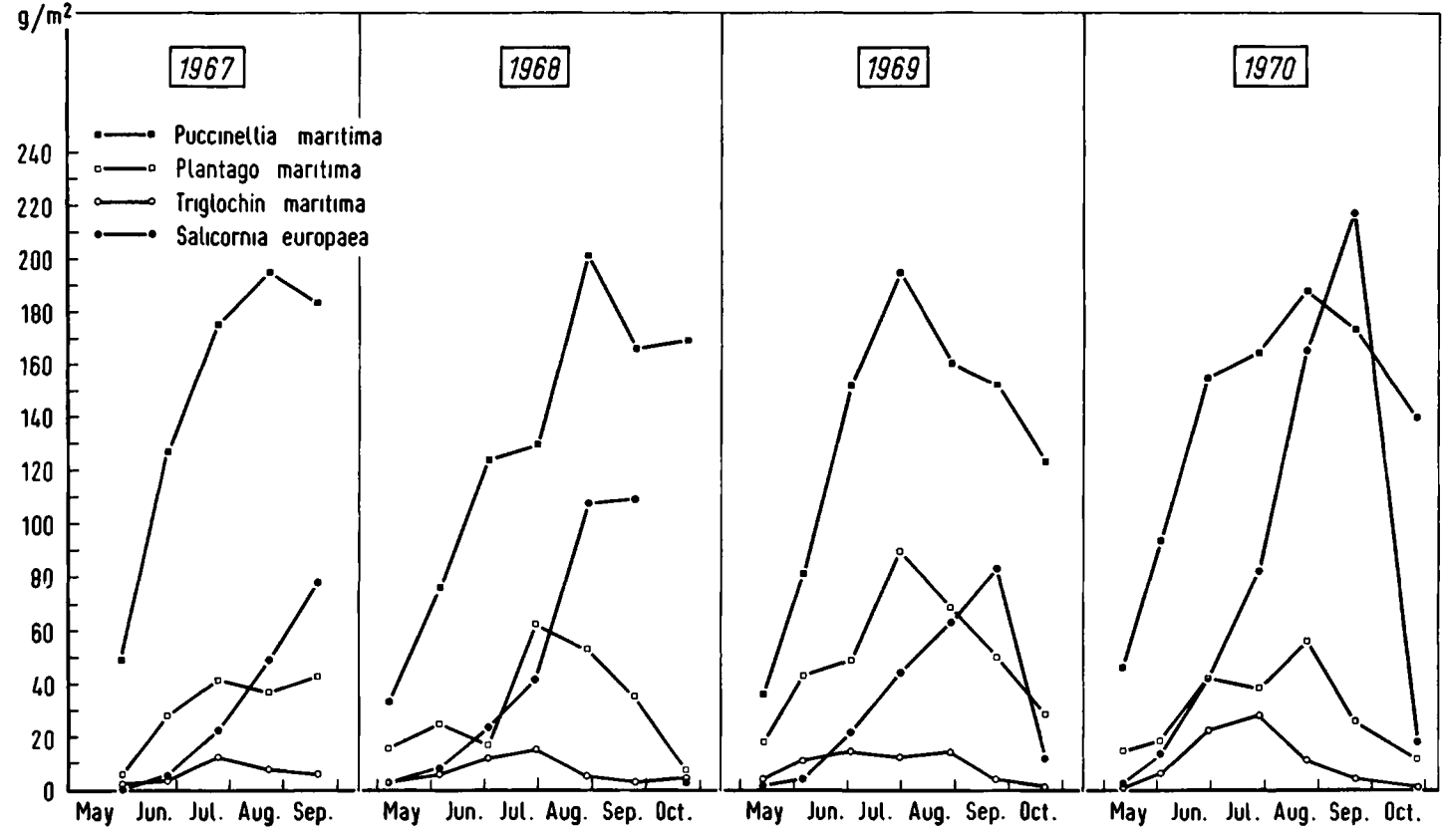

Fig.14. Changes in standing crop of important species in ungrazed (in enclosures) *Puccinellietum maritimae*, from 1967 to 1970 inclusive

than in the other years; the plants flowered well. In 1970 *Plantago* flowered noticeably little but leaf mortality was low (cf. PL); the maximum biomass was found in August that year.

The curves for the development of *Tr. maritima* in PM are similar to those for PL. There is a peak in biomass in July. An increase in biomass from 1967 to 1970 is evident. As stated previously, some other species, not shown in fig.14, occur regularly in the samples, but they constitute only a small proportion of the total living biomass (see table 19). On the other hand, there are also species which occur occasionally, but constitute up to 5% of the total living biomass, e.g. *Juncus gerardii* and *Spartina townsendii.*

When the curves for the total living biomass are compared with those for a few of the most important species, then it is clear how these species determine the curves for the living biomass. In July 1969 *Pucc. maritima* and *Pl. maritima* had reached their peak in the total living biomass. Both species then decreased in biomass and two months later *Salicornia* had a peak in the standing crop; due to this a second peak in the curve for living biomass is seen. In 1970 the August peak in total living material continues until September, but then it is determined by *Salicornia*, while in August it is determined by *Pucc. maritima* and *Pl. maritima*.

TABLE 20

Frequency of occurrence of the species (in percentages) in the total number of cut samples (of 0.125 m^2) in *Puccinellietum maritimae*

	1968	1969	1970
Total number of cut samples	67	70	70
Puccinellia maritima	100	100	100
Plantago maritima	92	91	97
Triglochin maritima	72	54	67
Spergularia media	94	96	100
Salicornia europaea	97	99	100
Suaeda maritima	79	86	97
Aster tripolium	66	90	83
Limonium vulgare	24	50	57
Glaux maritima	16	19	19
Spartina townsendii	10.5	11	20
Cochlearia anglica	6	3	4
Halimione portucaloides	4.5	13	1
Halimione pedunculata	–	–	1
Carex extensa	4.5	–	–
Juncus gerardii	7.5	7	4

Table 20 gives the frequency of occurrence of the species in the samples in the various years; 1967 was not calculated because there were less harvests that

year. The majority of species show no change in occurrence during the course of the years. *Pucc. maritima, Sal. europaea, Pl. maritima, Tr. maritima* and *Sper. media* are the plants which occur most frequently. There is a noticeable difference in the occurrence of *L. vulgare*; in 1968 the species was only present in 24% of the investigated samples; in 1970 in 57%. Many *Limonium* plants probably died under the influence of grazing during the very wet season of 1966. Subsequently there was a long recovery period.

The occurrence of *Sp. townsendii* and *A. tripolium* has also increased. It appears here also that an increase in occurrence does not necessarily imply an increase in weight at the same time (cf. table 19 with table 20).

The performance of the species is mainly dependent upon the intensity of grazing in the previous season.

PUCCINELLIETUM MARITIMAE – Grazed

During the years of investigations the cattle were fenced in on May 18th, 1967, ± May 11th, 1968, May 12th, 1969 and May 25th, 1970. The number of cows (mainly yearlings) was always ± 120 (Van der Zijpp, 1971). Horses were also sometimes present (± 10). Because the studied area is only a small part of the total, very varied pasture, the cattle do not graze continuously here.

The first samples outside the enclosures were taken ± 1 month after grazing had started. The values of the biomasses for May (see table 19) are therefore similar to those from the enclosures.

In October the harvested material could no longer be separated into dead and living material due to its bad condition. In August 1969 no samples could be taken at all due to very bad site conditions. The harvesting of the plants outside the vegetation cages was more difficult than inside the cages, especially when the site was wet after flooding or rain. Much material is trampled and the soil surface is very irregular with many holes (due to the hooves of cattle and horses).

Dead and living material

The curves for the dead and living material of the various years (fig.15) agree very well with each other, but also with those for the material from the enclosures (cf. fig.15 with fig.13). The smallest amounts of dead and living material were found in spring. There are maximum amounts of dead material in October; the maximum values for living material are in July or September. The latter is in contrast to the enclosures where the maximum values were found in August.

All the values for the dead and living material are lower than when it is

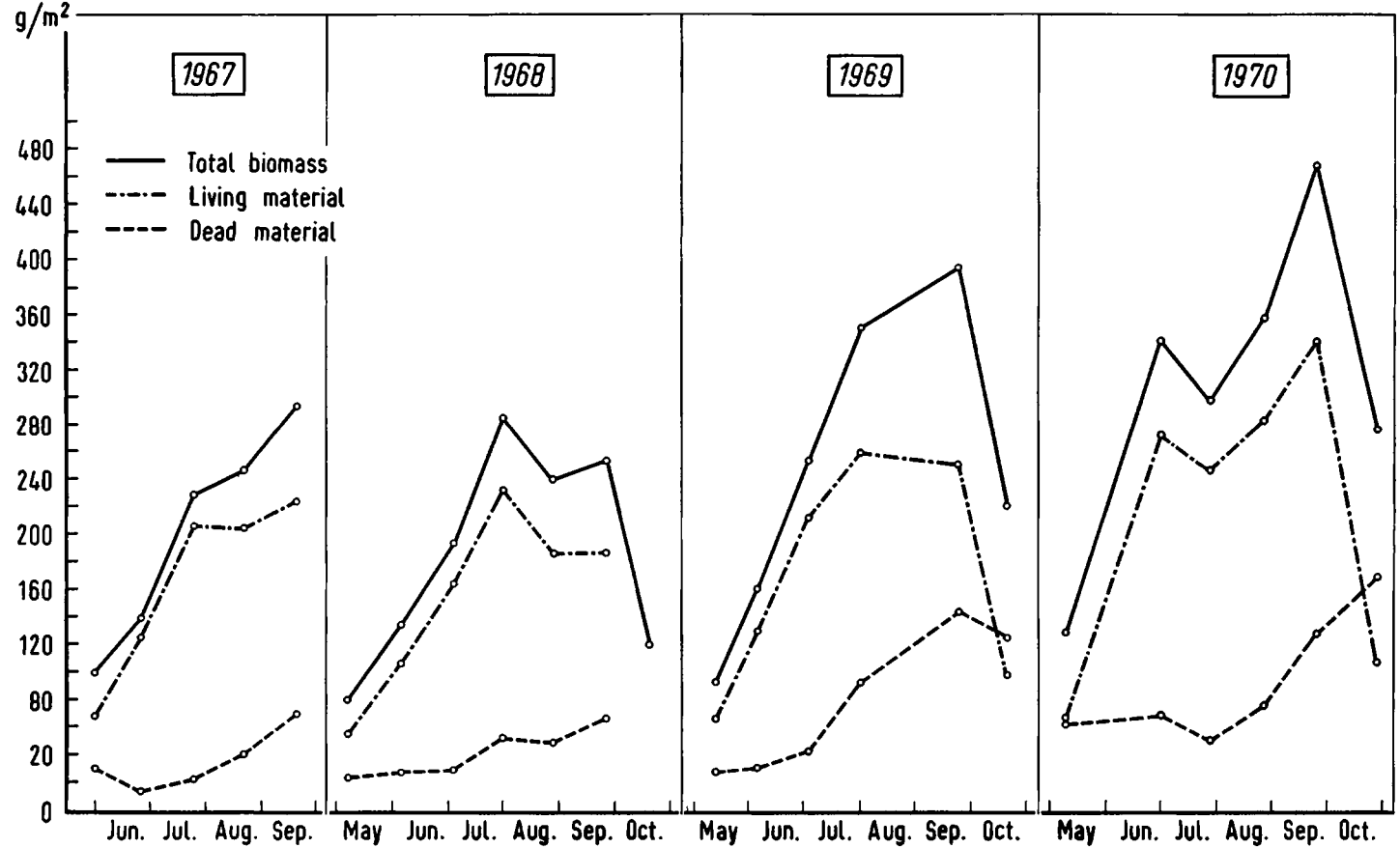

Fig.15. Changes in standing crop of above-ground material in grazed *Puccinellietum maritimae*, from 1967 to 1970 inclusive

ungrazed. As a result of grazing the living material is removed from the area; less green material results in less dead material. In addition a lot of material is trampled in this wet area and covered with mud and can then hardly be collected.

The development in 1970 is remarkable. More green material (273 g/m^2) is present in June of that year than the maximum values of the previous years, and almost as much as in the enclosures. After a retrogression in June-July the living material increases and reaches a maximum in September (342 g/m^2). This is presumably due to the fact that in 1970 the cattle came into the meadow later than in the other years (see above), and that in addition the area was drier than in the past (little precipitation; higher temperatures). The vegetation covering was already well developed and less vulnerable to grazing. The influence of grazing was not evident until July.

Floristic composition

The same species were found as in the enclosures. All dry weights, however, are much lower (table 19). Here also *Pucc. maritima, Pl. maritima* and *Sal. europaea* form 85%-90% of the living biomass. At the beginning of the season *Pucc. maritima* and *Pl. maritima* are the most important species. In September *Sal. europaea* can constitute up to 46% of the living biomass.

The proportion of *Pucc. maritima* in the total living biomass is generally a few percent higher than in the enclosures. The curves for the most important species are shown in fig.16. The maximum values of the species are reached almost at the same times as in the enclosures. The development of *Pl. maritima* and *Tr. maritima* is very poor in 1970. The maximum values of *Pucc. maritima* vary from 129 g/m^2 to 180 g/m^2. The high value in June 1970 is very noticeable, higher even than in the enclosure (180 g/m^2 and 154 g/m^2 resp.). *A. tripolium, Su. maritima, Sp. townsendii* and *L. vulgare* occur in much smaller quantities than in the enclosures. Their maximum biomass is only half of that inside the vegetation cages. Consumption by cattle was clearly seen for *Pucc. maritima, Sp. townsendii* and *A. tripolium* but not for *L. vulgare, Su. maritima* or *Sal. europaea.* The decrease in material for the last three species must be attributed to trampling.

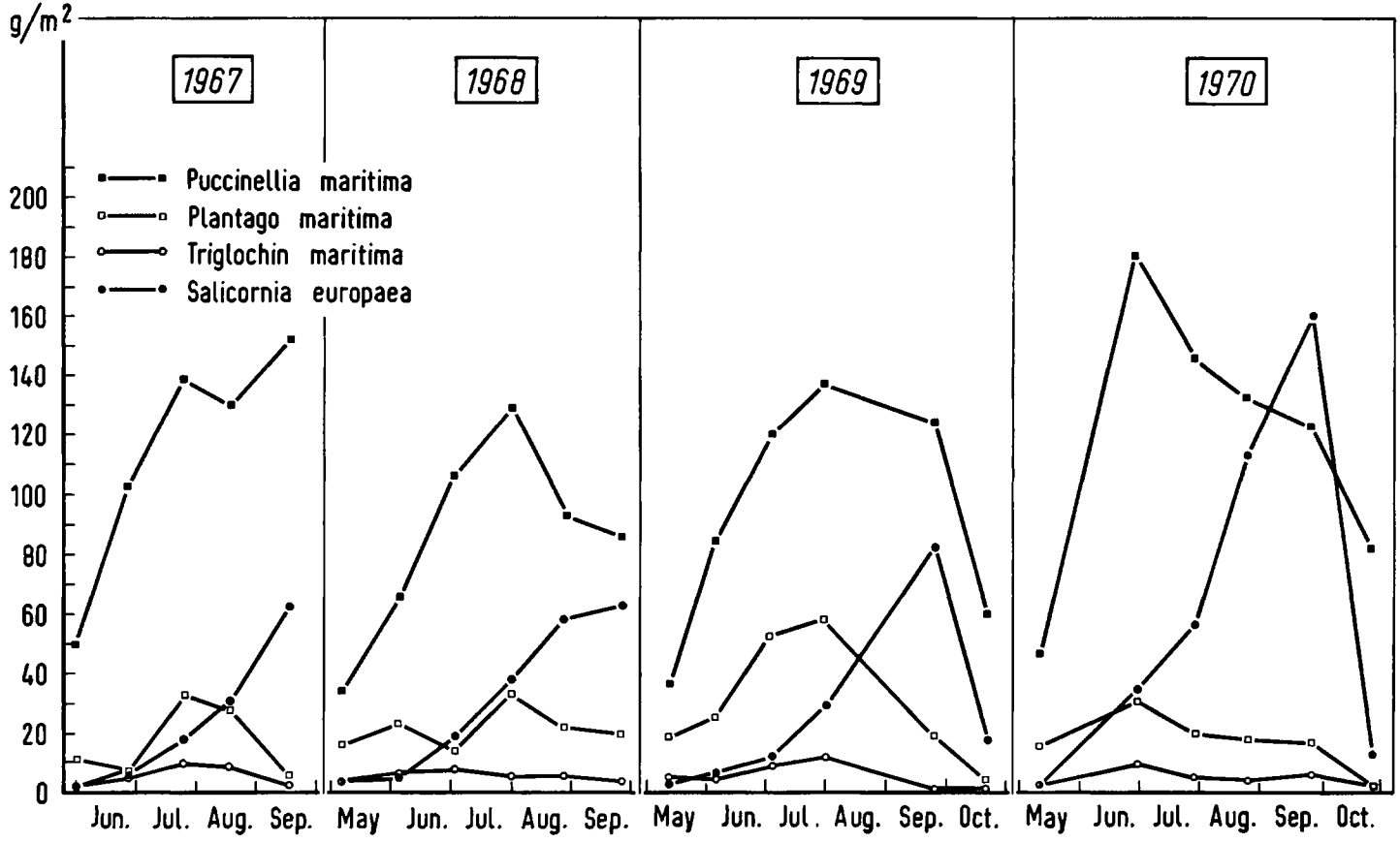

Fig.16. Changes in standing crops of important species in grazed *Puccinellietum maritimae*, from 1967 to 1970 inclusive.

TABLE 21

Statistical variation of green material, dead material and total vegetation in 1968 and 1969 in *Junco-Caricetum extensae* subass. *blysmetosum rufi*, *Plantagini-Limonietum* and *Puccinellietum maritimae* (ungrazed)

year	date	green material										
		n	$\bar{x}$	min.	max.	σ	S.E.M.	%S.E.M.	C.V.	n	$\bar{x}$	min.
JUNCO-CARICETUM EXTENSAE subass. BLYSMETOSUM RUFI												
1968	17/4	15	7.57	2.80	17.64	4.05	1.04	14	54	15	32.76	22.10
	13/5	15	10.85	1.62	22.45	4.84	1.25	12	45	15	14.18	8.22
	10/6	15	24.02	11.81	38.11	6.08	1.57	6	25	15	13.35	8.42
	8/7	15	37.38	20.13	59.42	9.67	2.50	7	26	15	13.20	7.65
		20	35.55	18.96	59.42	10.12	2.26	6	28	20	12.63	7.65
	5/8	15	36.39	19.84	51.71	9.57	2.47	7	26	15	12.51	6.27
	2/9	15	34.91	20.38	51.30	7.22	1.86	5	21	15	10.27	5.83
	30/9	15	28.23	12.84	39.62	7.22	1.86	7	26	15	15.94	7.13
	16/10	10	17.48	8.46	48.33	11.39	3.60	21	65	10	15.48	9.95
1969	16/4	15	3.87	1.34	11.74	2.32	0.60	16	60	15	15.63	8.90
	14/5	15	14.86	6.99	21.31	4.51	1.66	11	30	15	19.49	11.60
	10/6	15	27.01	17.88	39.01	5.40	1.40	5	20	15	15.64	7.85
	8/7	15	39.00	28.77	52.97	6.73	1.74	4	17	15	16.59	6.62
	5/8	15	43.25	33.03	56.09	7.50	1.94	4	17	15	21.73	9.22
	2/9	15	35.41	19.06	51.68	8.85	2.29	6	25	15	16.88	9.38
	3/10	15	26.50	16.47	40.87	6.00	1.55	6	23	15	22.70	15.02
PLANTAGINI-LIMONIETUM												
1968	24/4	15	9.22	6.15	13.84	2.01	0.52	6	22	15	14.17	3.62
	21/5	15	17.10	13.98	20.95	1.99	0.51	3	12	15	8.89	5.30
	17/6	15	37.70	25.98	50.32	5.42	1.40	4	14	15	11.85	3.23
	15/7	15	46.56	31.50	56.13	6.22	1.61	3	13	16	12.55	4.90
	12/8	15	58.21	52.57	68.23	4.74	1.56	3	8	15	17.14	9.20
	9/9	15	40.53	26.46	65.40	9.45	2.44	6	23	15	24.67	12.51
	7/10	15	9.70	4.98	12.79	2.00	0.52	5	21	15	36.02	26.74
1969	21/4											
	20/5	14	13.19	8.30	16.76	2.32	0.62	5	18	14	30.53	15.95
	17/6	15	36.48	28.92	45.31	4.97	1.28	4	14	15	25.42	10.59
	15/7	15	49.58	36.54	61.97	6.95	1.80	4	14	15	23.22	14.88
	12/8	10	48.44	38.21	53.37	9.13	2.89	6	19	10	32.49	22.15
	9/9	10	26.06	17.35	41.07	7.95	2.52	10	31	10	38.21	29.18
	17/10	10	14.77	10.56	20.08	2.62	0.83	6	18	10	46.43	31.96
PUCCINELLIETUM-MARITIMAE												
1968	6/5	10	6.96	2.29	11.48	3.12	0.99	14	45	10	3.06	1.92
	4/6	10	16.20	7.75	29.09	7.20	2.28	14	44	10	3.39	1.55
	1/7	10	24.03	13.95	31.18	4.95	1.56	7	21	10	4.18	2.89
	29/7	10	35.12	23.77	45.14	6.41	2.03	6	18	10	7.31	4.06
	27/8	9	51.77	32.12	62.83	9.32	3.11	6	18	9	10.00	5.63
	25/9	9	45.68	24.59	74.80	15.72	5.24	11	34	9	15.70	4.93
	23/10	9	24.17	16.67	39.62	7.21	2.40	10	30	9	27.19	19.63
1969	12/5	10	8.22	4.95	11.38	2.13	0.67	8	26	10	3.34	0.97
	4/6	10	19.42	13.20	26.08	3.95	1.25	6	20	10	3.90	0.24
	2/7	10	33.05	25.59	42.84	6.08	1.94	6	18	10	5.03	2.57
	29/7	10	51.65	43.48	69.32	8.24	2.61	5	16	10	11.02	8.39
	27/8	10	46.65	27.97	74.64	12.47	3.95	8	27	10	11.62	6.55
	23/9	10	49.55	31.39	61.11	10.71	3.39	7	22	10	24.67	16.93
	21/10	10	22.84	13.35	31.68	6.44	2.04	9	28	10	32.11	12.94

Explanation of signs: n = number of samples; $\bar{x}$ = arithmetic mean of n samples (0.125 m^2); min. = error of mean ($\frac{\sigma}{\sqrt{n}}$); % S.E.M. = $\frac{\text{S.E.M.}}{\bar{x}} \times 100$; C.V. = coefficient of variation.

dead material					total vegetation							
max.	σ	S.E.M.	%S.E.M.	C.V.	n	x̄	min.	max.	σ	S.E.M.	%S.E.M.	C.V.
42.86	6.30	1.63	5	19	15	40.34	28.23	50.07	8.14	2.10	5	20
18.97	3.24	0.84	6	23	15	25.01	17.57	36.39	4.50	1.16	5	18
19.39	2.84	0.73	5	21	15	37.37	22.17	48.68	6.56	1.69	5	18
17.63	2.71	0.70	5	21	15	51.24	33.40	69.12	9.31	2.40	5	16
17.96	3.14	0.70	6	25								
24.96	4.18	1.08	9	33	15	48.90	26.11	63.46	9.32	2.41	5	19
14.24	2.73	0.70	7	27	15	45.19	30.18	65.54	10.44	2.70	6	23
36.05	6.64	1.72	11	42	15	44.17	22.07	58.78	9.75	2.52	6	22
22.13	3.60	1.14	7	23	15	32.96	19.54	66.18	12.61	3.99	12	38
22.40	3.52	0.91	6	23	15	19.50	11.64	29.36	4.69	1.21	6	24
30.35	4.52	1.17	6	23	15	34.34	24.92	40.79	5.30	1.37	4	15
22.57	3.98	1.03	7	25	15	42.64	29.84	54.94	7.33	1.89	4	17
24.38	5.17	1.34	8	31	15	55.59	36.77	73.99	10.51	2.71	5	19
32.06	6.63	1.71	8	31	15	64.98	48.34	87.63	13.02	3.36	5	20
26.92	4.68	1.21	7	28	15	52.29	35.15	76.97	12.02	3.11	6	23
35.33	5.29	1.36	6	23	15	49.20	38.45	63.25	8.28	2.14	4	17
33.53	8.18	2.79	20	58	15	23.39	10.57	43.08	9.44	2.44	10	40
13.04	2.48	0.64	7	28	15	25.99	20.53	32.36	3.71	0.96	4	14
22.77	5.68	1.47	12	48	15	49.35	31.76	60.67	8.89	2.30	5	18
23.13	4.58	1.18	9	36	15	59.11	39.94	70.94	9.05	2.34	4	15
25.72	4.98	1.29	8	29	15	75.35	64.24	92.34	8.51	2.20	3	11
39.15	6.55	1.69	7	27	15	65.20	38.97	98.34	12.92	3.34	5	20
48.15	6.16	1.59	4	17	15	45.72	34.33	60.03	7.26	1.88	4	16
					15	30.71	21.25	47.07	7.70	1.99	6	25
43.66	6.53	1.75	6	21	14	43.72	30.32	54.62	6.52	1.74	4	15
43.59	9.16	2.37	9	37	15	61.90	44.85	79.41	11.39	2.94	5	18
37.73	7.61	1.97	8	33	15	72.80	53.38	94.12	11.17	2.88	4	15
47.21	7.72	2.44	8	24	15	82.81	61.56	116.85	15.93	4.11	5	19
55.31	8.58	2.72	7	22	15	66.21	46.99	86.74	11.85	3.06	5	18
59.86	9.52	3.01	6	20	10	61.20	45.24	77.05	10.20	3.22	5	17
4.26	0.62	0.20	7	20	10	10.03	5.11	14.20	3.04	0.96	10	30
7.82	1.84	0.58	17	54	10	19.59	9.30	36.04	8.50	2.69	14	43
6.45	1.01	0.32	5	24	10	28.20	17.31	36.38	5.71	1.81	6	20
10.20	1.94	0.61	8	27	10	42.43	29.27	55.34	8.17	2.58	6	19
16.08	3.15	1.05	11	32	9	61.73	38.59	78.91	11.68	3.89	6	19
22.30	5.35	1.78	11	34	9	61.44	29.52	88.17	15.83	5.28	9	26
39.35	6.50	2.17	8	24	9	51.36	36.73	71.94	10.92	3.64	7	21
7.51	1.82	0.58	17	54	10	11.56	6.89	17.61	3.19	1.01	9	28
3.62	1.97	0.62	16	51	10	23.31	16.09	33.60	5.46	1.73	7	23
7.99	1.42	0.45	9	28	10	38.08	28.16	47.89	7.14	2.26	6	19
14.39	2.08	0.66	6	19	10	62.67	52.25	82.12	9.60	3.04	5	15
15.83	2.63	0.83	7	23	10	58.27	37.12	90.47	13.86	4.39	8	24
37.46	5.56	1.76	7	23	10	74.21	53.54	96.06	13.57	4.29	6	18
38.15	7.26	2.30	7	23	10	54.95	28.83	69.83	12.20	3.86	7	22

minimum biomass of series; max. = maximum biomass of series; σ = standard deviation; S.E.M. = standard

TABLE 22

Statistical variation of the most important species in 1969 in *Junco-Caricetum extensae* subass. *blysmetosum rufi*, *Plantagini-Limonietum* and *Puccinellietum maritimae* (ungrazed)

JUNCO-CARICETUM EXTENSAE subass. BLYSMETOSUM RUFI

Year	Date	Juncus gerardii						
		n	$\bar{x}$	min.	max.	σ	S.E.M.	%S.E.M.
1969	16/4	15	1.05	0.32	2.12	0.62	0.16	15
	14/5	15	5.91	0.74	12.20	3.50	0.90	15
	10/6	15	11.46	4.29	18.14	3.99	1.03	9
	8/7	15	16.82	6.22	36.28	9.41	2.43	14
	5/8	15	17.45	0.00	45.27	10.58	2.73	16
	2/9	15	13.24	0.00	37.22	9.08	2.35	18
	3/10	10	9.92	1.38	21.96	6.25	1.98	20

PLANTAGINI-LIMONIETUM

Year	Date	Plantago maritima						
		n	$\bar{x}$	min.	max.	σ	S.E.M.	% S.E.M.
1969	20/5	14	7.83	6.12	11.37	1.73	0.46	6
	17/6	15	20.07	9.08	31.51	6.96	1.80	9
	15/7	15	30.27	17.92	43.08	7.20	1.86	6
	12/8	10	30.78	19.00	41.91	7.13	2.26	7
	9/9	10	12.90	6.91	18.67	3.83	1.22	10
	7/10	10	6.50	3.86	10.02	2.12	0.67	10

PUCCINELLIETUM MARITIMAE

Year	Date		Puccinellia maritima					
		n	$\bar{x}$	min.	max.	σ	S.E.M.	% S.E.M.
1969	12/5	10	4.53	2.84	5.79	0.90	0.28	6
	4/6	10	10.20	6.73	13.60	2.20	0.70	7
	2/7	10	19.02	5.05	24.27	5.60	1.77	9
	29/7	10	24.36	12.09	35.41	6.91	2.19	9
	27/8	10	20.12	15.35	31.88	5.30	1.70	8
	23/9	9	20.65	12.97	30.32	4.88	1.63	8
	20/10	10	15.40	6.82	22.58	5.24	1.66	11

Explanation of signs:

n = number of samples; $\bar{x}$ = arithmetic mean of n samples (g/0.125 m^2); min. = minimum biomass of series; max. = maximum biomass of series; σ = standard deviation; S.E.M. = standard error of mean ($\frac{\sigma}{\sqrt{n}}$); % S.E.M. = $\frac{\text{S.E.M.}}{\bar{x}} \times 100$; C.V. = coefficient of variation.

	Plantago maritima							
C.V.	n	$\bar{x}$	min.	max.	σ	S.E.M.	%S.E.M.	C.V.
59	15	1.00	0.00	3.47	1.02	0.26	26	102
59	15	5.06		14.74	5.45	1.41	28	108
35	15	8.12	0.00	22.53	7.80	2.02	25	96
56	15	9.78	0.00	29.71	8.99	2.32	24	92
61	15	13.37	0.05	36.37	11.49	2.97	22	86
69	15	11.19	0.20	34.40	8.77	2.27	20	78
63	10	8.62	0.77	15.37	5.30	1.68	19	61

	Limonium vulgare							
C.V.	n	$\bar{x}$	min.	max.	σ	S.E.M.	% S.E.M.	C.V.
22	14	2.55	1.63	4.16	0.77	0.21	8	30
35	15	10.78	4.51	22.10	4.54	1.17	11	42
24	15	11.81	5.87	18.31	4.00	1.03	9	34
23	10	11.65	6.03	24.23	5.37	1.70	15	46
30	10	6.44	1.16	16.98	5.17	1.64	25	80
33	10	4.17	1.84	6.77	1.78	0.56	13	43

	Salicornia europaea							
C.V.	n	$\bar{x}$	min.	max.	σ	S.E.M.	% S.E.M.	C.V.
20	10	0.19	0.02	0.42	0.13	0.04	21	68
22	10	0.53	0.04	1.01	0.38	0.12	23	72
29	10	2.76	0.73	6.22	1.92	0.61	22	70
28	10	5.59	2.24	10.56	2.33	0.74	13	42
27	10	7.92	2.63	16.76	3.93	1.24	16	50
24	10	10.39	5.17	18.97	4.06	1.28	12	39
34	10	1.49	0.00	4.54	1.48	0.47	32	99

In order to gain an impression about the variation in the biomasses of the samples of each series, a few statistical calculations were made. The standard deviation, the standard error of the mean (S.E.M.) and the coefficient of variation were calculated (cf. Moroney, 1962). This was done for the living material, the dead material and the total vegetation of the samples of 1968 and 1969, and for the most important taxa of each biotope of the samples of 1969. The results of these calculations will not be discussed in detail because the statistical processing of all data will appear elsewhere in connection with the results of other IBP-projects.

Table 21 gives the calculated statistical parameters, concerning the dead material, the living material and the total vegetation. These calculations show that the variation in the total biomass of the samples of a series is smaller than in the separate categories, dead and living. The variation in the living material in general is again smaller than in the dead material.

The standard errors of the mean are in general not large in the experiments; they fluctuate from 4%-20% for the dead and living material and from 3%-14% for the total vegetation. The number and size of the samples in the investigated associations appear, therefore, to have been sufficient each time (cf. Jankowska, 1967; Traczyk, 1968). Large standard errors (> 10%) were mainly found in the samples of spring and autumn. This presumably largely coincides with the fact that in these seasons the biotopes are very often wet. The cutting of plant material is therefore made more difficult because the dead material is mixed with mud end because it is not always possible to determine precisely whether or not it is cut at ground level. A greater error in harvesting is made here than when a thick vegetation covering has developed and the area is dry. The larger variation in the biomass of the samples of PM in June 1968 is also a result of harvesting errors; the experimental plot was inundated during the cutting of the samples.

The data given in table 22 show that the quantitative variation in the biomasses of the separate species in the samples of each series is much greater than in the biomass of the living or dead material. The biomass of a species in one sample can be several times greater than in another sample of the same set (cf. minimum and maximum value per harvest of the different species). The individuals of each taxa are not spread uniformly over the whole biotope and are not all in the same stage of development. Values of up to 107% were found for the coefficient of variation (see e.g. *Pl. maritima* in JC).

Table 23 shows estimations of the total net primary production, calculated according to different methods. Column 3 of this table gives the maximum values of living material in the standing crop as a measure of the net production. Two periods of change in the standing crop can be distinguished in the development of the three investigated communities. First a period of great increase (growth) followed by a sharp decrease in living material after a peak had been reached. Assuming that there is no living material in the winter and that the biomass is harvested at its peak, this maximum can be a good approximation of the true net production. By using this agricultural method of determining production, however, it is assumed that all the individuals of each species reach their maximum at more or less the same time. This situation can almost be reached with mono-cultures. This is not the case with natural vegetations. The data in tables 10, 14 and 19 show that the different species of each biotope reach their maximum biomass at different times. A second possibility, therefore, of obtaining an impression of the size of the primary production, is to add the maximum biomasses of the species together. The values obtained in this way are given in column 4 of table 23. The smaller differences in JC and PL with the values given in column 3 (an average of 11% and 8% higher resp.) can be seen. The averages of PM and PM-A are much higher (16% and 22% resp.).

As already described, in the results concerning the changes in standing crop, it was established that 80%-90% of the living biomass is determined by only 2 or 3 dominant species, it is obvious, therefore, that the maximum of living material is also determined by the maximum of these dominant species. This is further confirmed when the values of column 4 are compared with those of column 3. When the differences are small, the maximum of the living material coincides with the maximum of one or more dominant species. This is usually the case in JC and PL; moreover for these sites it appeared that the maximum values of the dominant species are maintained, with small fluctuations, for a longer time. The same applies for PM in 1967 and 1968 (see table 23). Large differences, however, appeared in PM in 1969 and 1970, when the two most important species, *Pucc. maritima* and *Sal. europaea*, clearly reached their maximum values at completely different times, and which in addition were only of short duration. The sum of the maximum values of the species in these cases is noticeably higher than the maximum of the total biomass. The greatest differences between the maximum standing crop and the sum of the maximum values of the species are found in the grazed PM (12%-29%; average 22%). The development of the plants is strongly influenced by grazing; due to the same factor, the dates of maximum standing crop of the various species are more

TABLE 23

Total net primary production in g/m^2 of three salt-marsh communities, calculated in different ways (For explanation: see text.)

Column no.: 1	2	3	4	5	6	7	8
Site	year	Max. standing crop green material	Sum max. standing crop of separate species	$\Sigma(\Delta a+\Delta b)$	% increase column 4 over 3	% increase column 5 over 3	% increase column 5 over 4
Junco-Caricetum extensae subass. blysmetosum rufi	1967	343	297	295	22	21	-
	1968	291	320	291	9	–	- 9
	1969	346	372	395	7	14	6
	1970	329	352	397	7	21	13
average		302	335	344	11	14	3
Plantagini-Limonietum	1968	466	486	532	4	14	10
	1969	397	424	462	6	16	9
	1970	452	509	547	12	21	8
average		438	473	514	8	17	9
Puccinellietum maritimae (enclosures)	1967	335	357	389	6	16	9
	1968	414	455	469	10	13	3
	1969	413	512	602	24	46	18
	1970	464	556	527	20	14	– 6
average		406	470	497	16	22	6
Puccinellietum maritimae (grazed)	1967	228	273	289	19	27	6
	1968	233	262	278	12	19	6
	1969	260	335	367	29	41	10
	1970	342	426	451	25	31	6
average		266	324	346	22	30	7

diverging. Also, the time interval of the maximum of one species changes from year to year; the maximum for e.g. *Pucc. maritima* varies from June to September.

The net primary production is determined by only a few dominant species. In JC, *J. gerardii, Pl. maritima* and, to a lesser extent, *Sc. rufus* are the species making up the bulk of the total production; 10-15 other species contribute less than 1% to the production. In PL, *Pl. maritima* and *L. vulgare* are the dominant species; in this biotope 8-10 species contribute less than 1% to the production. In PM, *Pucc. maritima, Sal. europaea* and *Pl. maritima* together supply a good 85% of the production; a small number of species, 2-4, contributes less than 1%. So the annual differences in production are then largely reduced to a difference in the biomass of one or more of these dominant species. This can be seen when tables 10, 14 and 19 are compared with the production figures of table 23. For example, the difference in production in 1968 and 1969 in PL (486 and 424 g/m^2 resp.) is determined by the large production of *Pl. maritima* in 1968; the maximum of *L. vulgare* is the same in both years. In 1970, on the other hand, the increase in production compared with 1969 can be attributed to the large increase of *Limonium*; the maximum values of *Plantago* are almost the same for 1969 and 1970. In PM it can be seen even more clearly how 1 or 2 species can influence the total net production. Here, the maximum standing crop of *Pucc. maritima* is nearly the same for all the years (187-201 g/m^2), that of *Pl. maritima* and *Sal. europaea*, however, varies. The high total production in 1970 (555 g/m^2) is a result of the high production of *Salicornia* in that year. In 1969 *Plantago* as well as *Aster* (8%) and *Suaeda* (4%) contribute more to the total production than in other years.

In the PM-A area the contributions of the most important species to the total production, in percentages, are almost as large as in the enclosures.

In 1970 not only did *Salicornia* have a greater production in PM-A but even the maximum standing crop of *Puccinellia* was greater than in the previous years. So the net production in 1970 is higher than in previous years.

The values given in column 4 of table 23 show that PM-A is the least productive (average of 324 g/m^2). The highest production was found in 1970 (426 g/m^2); the least productive was 1968 with 262 g/m^2. After PM-A comes JC, where the production varied from 297-370 g/m^2 (average of 335 g/m^2). The average production in PL and in the enclosures of PM is about the same (473 and 470 g/m^2 resp.). In PL smaller variations in production were found than in PM (424-509 g/m^2 and 357-555 g/m^2 resp.).

There are also some objections to this method of calculating the production figures, and the values obtained are probably underestimated. Firstly it is assumed that all individual plants of one species reach their maximum standing crop at the same time. This is never so under non-agrarian conditions. Data

from the first and last found flowering specimens of one species are sometimes separated by an interval of two months. In fact, only an average maximum of all individuals is determined. Secondly it is not certain whether the maximum obtained for the standing crop is the true one or whether this must be attributed to spatial variation in the vegetation. The distribution of species over the area is not uniform, so that a peak can occur when, by change, many plants of one species appear in a few samples from one harvest. It appears from phenological observations, however, that the maximum of the most important species, i.e. those which are frequently found in the samples, falls inside a time interval which coincides with their optimum development (July-August). The maximum standing crops, however, found for those species which do not occur frequently, or if so then only in very small amounts, are not always representative but are sometimes accidental such as, for example, *J. gerardii* and *Sp. townsendii* in PM; or *Agrostis stolonifera* in JC (in 1967), or in PL *J. gerardii, C. extensa* and *F. rubra*. These species generally, however, only contribute very little to the total production. The third objection is that it is not certain whether harvesting takes place exactly during the peak or whether just before or after. The intervals between two harvests could have been too long, which is perhaps shown in those species where the maximum continues, with a few fluctuations, for a longer time; such as, for example, *J. gerardii* in JC, *Pl. maritima* in JC and PL. This can also be the result of the difference in development between leaf and flowering parts, as has already been shown in tables 12 and 17 for *J. gerardii* and *L. vulgare* respectively. The production figure for JC in 1970 is definitely underestimated as a result of the long intervals between two harvests. The maximum values obtained there for the different species are not always the true ones.

Finally, the fact that the mortality of green plant parts is not taken into account, either before or after the peak in biomass has been reached, is another objection which must be mentioned. This objection also applies to the production figures given in column 3 of table 23. All the green plant parts photosynthesise, even in periods in which the total biomass decreases due to death or to the translocation of materials to the roots.

In column 5 of table 23 production figures are given in which attempts are made to take into account the death of green material. For it can be stated that the real increase of living material, in a specific period, is the same as the difference between the amounts of material at the beginning and end of this period (= Δb) plus the amount of green material which dies in this period (Wiegert & Evans, 1964). This mortality may be seen in principle as an increase in dead material (+ Δa). In other words the production over a specific period is, therefore, the difference in amounts of living material at the beginning and end of that period respectively plus the increase in dead material. The total produc-

tion over the whole season is the sum of the positive values of $\Delta b + \Delta a$. In order to simplify the calculation, it has been assumed here that the amount of living material, present in the first harvest (April or May), has grown in the preceding weeks and has not remained over from the previous autumn. It cannot be ascertained to what extent this is correct, because harvesting before April was not possible due to bad site conditions.

The production figures of column 5 are the same or a little higher than those of column 4; only occasionally are they lower. The average values are all higher (3%-9%), although for JC only very slightly. The difference in PL is very constant; in JC and PM the differences show a greater variation. The highest production in PM, 602 g/m^2, is now found in 1969 and not, as calculated in column 4, in 1970. The averages for PL and PM are again the same (513 and 497 g/m^2 resp.) as are the averages for JC and PM-A (344 and 335 g/m^2 resp.).

The difference in production between PM and PM-A is not constant (cf. the values from column 5 in table 23), but varies from 77 g/m^2 to 235 g/m^2. The size of this difference is dependent upon the extent of grazing and the condition of the site. When the site is wet, resulting from a lot of rain and/or frequent floods, as e.g. in 1968, the loss in production as a result of trampling is greater than when the site is dry. The large difference in production between the grazed area and the enclosures in 1969 is presumably due to flooding at the beginning of the season (June), and partly also due to the fact that the production for the grazed area is underestimated. Harvesting could not take place in August of that year. In 1970 the vegetation suffered less from trampling, as the cattle only came into the field at the end of May.

TABLE 24

Net primary production values in *Plantagini-Limonietum* in 1970, calculated from the changes in the living material and in the newly-formed dead material (Values in g/m^2)

Period		Number of days	Changes in dead biomass	Changes in green biomass	Production in g/m^2	
					for period	per day
	until May 19th →	?	+ 6	+188	194	
May 19th	– June 16th	28	+ 13	+159	172	6.15
June 16th	– July 15th	29	+ 13	+103	116	4.02
July 15th	– Aug. 12th	28	+ 38	+ 2	40	1.41
Aug. 12th	– Sep. 7th	26	+113	– 28	85	3.46
	Total				607	

It should be pointed out that the total amount of dead material (that from previous years plus the newly-formed) was determined monthly. In some periods between two harvests the decrease of this old, dead material could be due

to the fact that the decomposition by micro-organisms was greater than the increase as a result of the mortality of living material. This increase is in that case not included in the production calculations. This is clearly illustrated by table 15 in which the changes of the old, dead material and the newly-formed are given for PL. When only the increase in newly-formed, dead material is used for the production calculations together with the changes in green material, then the production amounts to 607 g/m^2, thus considerably more than when the differences in the total dead biomass are considered (547 g/m^2; see tables 24 and 23 resp.). It is not ascertained from these data to what extent decomposition takes place in the newly-formed, dead material.

PRODUCTION RATES

Table 25 gives the production rates for the different periods between the harvests. These values are obtained by the increase in dead material plus the increase in living material, divided by the number of days in the period (cf. Sesták & Čatsky, 1966; Kelly et al., 1969). The growth rates for a few of the most important species of each vegetation type are also shown in this table; these are calculated from the increase in living material in the period concerned.

The fastest growth in JC is in May. The growth rates in this period are similar and vary from 3.91 g/m^2/day to 4.25 g/m^2/day. The fact that in 1967 and 1970 harvesting took place at different times than in 1968 and 1969, must be taken into account when comparing the growth rates. The growth rate is also high at the beginning of the summer, during the time of flowering and fruit setting (3.29 g/m^2/day in 1968; 3.84 g/m^2/day in 1969). After the second half of August there is scarcely any further growth.

The figures for the growth rate for the April-May period 1969 are presumably too high. The determinations of the increase in dead material led to numbers which are much too high for the time of the year. The dead material in April or in May 1969 was probably inaccurately collected. On the basis of the increase in living material only, the growth rate amounts to 3.14 g/m^2/day. *J. gerardii* shows a maximum daily growth in late spring and early summer (May-July period), when considerable leaf growth is followed by the development of flowering parts. After July there is only slight growth. The other species (*Plantago* and *Scirpus*) also grow until the middle of the summer and have one period with maximum growth rate. *Scirpus* has its maximum growth in May-June; for *Plantago* this period varies (May-June in 1968; July-August in 1969).

The almost constant, high growth rate of PL in the May-June period (6.63-6.72 g/m^2/day) is striking. It is due to the rise in temperature and to the

TABLE 25

Net production rates for the living biomass of some salt-marsh communities and for the most important taxa in each biotope (Values in g/m^2)

JUNCO-CARICETUM EXTENSAE SUBASS. *BLYSMETOSUM RUFI*

Year	Period	Number of days	Production				
			Total living biomass		most important taxa per day		
			Per period	Per day	Juncus gerardii	Plantago maritima	Scirpus rufus
1967	until Apr. 24th	–	72,25	–	–	–	–
	Apr. 24th – May 25th	31	37.25	1.20	0.65	0.47	0.32
	May 25th – June 22th	28	119.24	4.25	1.39	0.16	1.14
	June 22th – July 20th	28	41.27	1.47	0.56	0.47	0.34
	July 20th – Aug. 16th	27	24.87	0.92	–	0.84	–
	Aug. 16th – Sep. 14th	29	–		–	0.17	–
	Sep. 14th – Oct. 16th	30	–	–	–	–	
1968	until Apr. 17th		60.61				
	Apr. 17th – May 14th	27	26.07	0.97	0.77	0.16	0.10
	May 14th – June 10th	27	105.52	3.91	1.81	1.09	0.69
	June 10th – July 8th	28	92.17	3.29	1.95	0.75	0.28
	July 8th – Aug. 5th	28	6.74	0.24	–	0.00	0.24
	Aug. 5th - Sep. 2nd	28	–	–	–	–	
	Sep. 5th – Sep. 30th	28	8.15	0.29	–		–
	Sep. 30th – Oct. 16th	16	–	–			-
1969	until Apr. 16th	–	30.95	–	-		
	Apr. 16th – May 14th	28	118.79	4.24	1.39	1.16	0.26
	(May 2nd May 14th)	(12)	(76.67)	(6.38)	(2.20)	(2.86)	(0.38)
	May 14th – June 10th	27	97.21	3.60	1.64	0.91	0.86
	June 10th – July 8th	27	103.60	3.84	1.53	0.47	0.73
	July 8th – Aug. 5th	28	75.10	2.68	0.18	1.03	–
	Aug. 5th – Sep. 2nd	28	–	–		–	
	Sep. 2nd – Oct. 3rd	31	–	–	–	–	
1970	until Apr. 24th	–	50.42				
	Apr. 24th – June 8th	45	242.67	5.39	2.85	0.54	–
	June 8th – Aug. 3rd	56	104.14	1.86	1.21	0.49	–
	Aug. 3rd – Oct. 1st	58	–	–		0.16	–

vegetation covering closing up in a short space of time. The growth rate is also high in the June-July period. In the July-August period of 1968 considerable growth took place once more, presumably due to fruit setting and seed ripening after abundant flowering of *Pl. maritima*. In other years the growth during this period was less. Only in 1970 was growth observed in the August-September period (1.77 g/m^2/day). Not only *Plantago*, but also a variety of other less

TABLE 25 (continued)

PLANTAGINI-LIMONIETUM

Year	Period	Number of days	Production				
			total living biomass		most important taxa per day		
			per period	per day	Plantago maritima	Limonium vulgare	Triglochin maritima
1968	until Apr. 24th	–	73.76	–	-	-	
	Apr. 24th – May 21st	27	63.04	2.33	0.85	1.00	0.13
	May 21st – June 17th	27	181.57	6.72	3.71	1.24	0.33
	June 17th – July 15th	28	83.83	2.99	2.25	0.77	–
	July 15th – Aug. 12th	28	130.18	4.65	3.11	0.17	0.02
	Aug 12th – Sep. 9th	28	–	–	-	–	-
	Sep. 9th – Oct. 7th	28	–	–	–	–	–
1969	until May 20th	–	105.52	–	–	–	–
	May 20th – June 17th	28	186.26	6.65	3.50	2.35	0.11
	June 17th – July 15th	28	104.89	3.75	2.91	0.29	0.28
	July 15th – Aug. 12th	28	65.06	2.32	0.15	–	–
	Aug. 12th – Sep. 9th	28	–	–	–	–	–
	Sep. 9th – Oct. 7th	28	–	–	–	0.65	–
1970	until May 19th	–	187.55	–	–	–	–
	May 19th – June 16th	28	185.76	6.63	1.86	2.94	0.40
	June 16th – July 15th	29	103.34	3.59	1.72	1.31	–
	July 15th – Aug. 12th	28	25.05	0.89	0.40	–	0.12
	Aug. 12th – Sep. 7th	26	46.02	1.77	0.61	–	0.23
	Sep. 7th – Oct. 5th	28	–	–	–	–	0.31

important species reached their maximum standing crop in September of that year.

The maximum growth rate of *Pl. maritima* and *L. vulgare*, the most important species in PL, coincides with the maximum growth rate of the total vegetation. There is often very little growth here after July. It has already been indicated that, during flowering and fruit setting of *Limonium* and *Plantago*, there is a large mortality of the leaves of these plants. This mortality surpasses the growth of the flowering parts (see also table 16).

The period of maximum growth rate in PM varies from year to year. The maximum values fluctuate from 4.24 g/m^2/day in 1967 to 7.29 g/m^2/day in 1969. In 1969 high values were always obtained, even as late as September when, during good weather conditions, the vegetation recovered from pro-

TABLE 25 (continued)

PUCCINELLIETUM MARITIMAE - Enclosures

Year	Period	Number of days	Production				
			total living biomass		most important taxa per day		
			per period	per day	Pucci-nellia maritima	Sali-cornia europaea	Plantago maritima
1967	until May 30th	–	62.68	–	–	–	–
	May 30th – June 26th	27	114.48	4.24	2.89	0.17	0.83
	June 26th – July 24th	28	96.39	3.44	1.72	0.63	0.49
	July 24th – Aug. 17th	24	71.12	2.96	0.83	1.09	–
	Aug. 17th – Sep. 19th	33	44.10	1.34	–	0.88	0.18
1968	until May 6th	–	55.71	–	–	–	–
	May 6th – June 4th	29	76.47	2.64	1.48	0.20	0.33
	June 4th – July 1st	27	68.93	2.55	1.77	0.59	–
	July 1st – July 29th	28	113.79	4.06	0.22	0.65	1.63
	July 29th – Aug. 27th	29	154.47	5.33	2.48	2.26	–
	Aug. 27th – Sep. 24th	28	–	–	–	0.07	–
	Sep. 24th – Oct. 23rd	30	–	–	0.11	–	–
1969	until May 12th	–	65.75	–	–	–	
	May 12th – June 4th	23	94.04	4.09	1.97	0.12	1.07
	June 4th – July 2nd	28	118.14	4.21	2.52	0.64	0.23
	July 2nd – July 29th	27	196.73	7.29	1.58	0.83	1.51
	July 29th – Aug. 27th	29	–	–	–	0.65	–
	Aug. 27th – Sep. 23rd	27	127.57	4.72	–	0.73	-
	Sep. 23rd – Oct. 20th	27	–	–	–	–	–
1970	until May 11th	–	66.71	–	–	–	–
	May 11th – June 1st	20	84.69	4.23	2.37	0.62	0.18
	June 1st – June 29th	28	152.61	5.45	2.19	0.98	0.86
	June 29th – July 27th	28	61.51	2.20	0.33	1.44	–
	July 27th – Aug. 24th	28	145.27	5.19	0.85	2.98	0.61
	Aug. 24th – Sep. 21st	28	16.08	0.57	–	1.86	–
	Sep. 21st – Oct. 26th	35	–	–	–	–	–

longed inundation in the last week of August. There was no growth in the July-August period of that year, unlike other years.

The maximum growth rate values for *Pucc. maritima* are very similar, but are found in different periods: 2.89 g/m^2/day and 2.52 g/m^2/day in June 1967 and 1969 respectively; 2.48 g/m^2/day in August 1968 and 2.37 g/m^2/day in May 1970. The value for the May-June period 1970 is calculated over only 20

TABLE 25 (continued)

PUCCINELLIETUM MARITIMAE - Grazed

Year	Period	Number of days	Production				
			total living biomass		most important taxa per day		
			per period	per day	Pucci-nellia maritima	Sali-cornia europaea	Plantago maritima
1967	until June 1st	–	69.88	–	-	-	–
	June 1st – June 27th	26	56.94	2.19	2.05	0.19	–
	June 27th – July 25th	28	89.61	3.20	1.27	0.41	0.91
	July 25th – Aug. 18th	24	17.19	0.72	–	0.52	–
	Aug. 18th – Sep. 18th	31	55.66	1.80	0.72	1.00	–
1968	until May 6th	–	55.71	–	–	–	–
	May 6th – June 4th	29	54.59	1.88	1.10	0.13	0.26
	June 4th – July 2nd	28	60.46	2.16	1.47	0.48	–
	July 2nd – July 30th	28	91.24	3.26	0.83	0.69	0.69
	July 30th – Aug 28th	28	–	–	–	0.74	–
	Aug. 28th – Sep. 25th	28	16.16	0.58	–	0.15	–
	Sep. 25th – Oct. 23rd	28	–		–	–	–
1969	until May 12th	–	65.75	–	–	–	–
	May 12th – June 5th	24	67.58	2.82	1.98	0.14	0.30
	June 5th – July 3rd	29	94.21	3.25	1.27	0.21	0.93
	July 3rd – July 30th	27	98.25	3.64	0.60	0.65	0.21
	July 30th – Sep. 24th	55	41.15	0.75	–	0 98	–
	Sep. 24th – Oct. 21st	27	–	–	–		–
1970	until May 11th	–	66.71	–	–	-	–
	May 11th – June 1st	20	84.69	4.23	2.37	0.62	0.18
	June 1st – June 29th	28	129.63	4.63	3.12	0.71	0.41
	June 29th – July 28th	29	–	–	–	0.76	–
	July 28th – Aug. 25th	28	59.25	2.11	–	2.05	–
	Aug. 25th – Sep. 25th	31	110.58	3.57	–	1.50	–
	Sep. 25th – Oct. 27th	32	–	–	–	–	-

days, so that a comparison with the other years is not completely accurate. The growth of *Sal. europaea* is very slight at the beginning of the season. It increases gradually until the largest growth rate is obtained in August. Only in 1969 did the growth rate fall somewhat in August, to be followed by an increase in September. In all the years of investigations growth can still be seen in the August-September period. The maximum growth rate of *Pl. maritima* in PM was reached in June (1967 and 1970) or July (1968 and 1969). There was no

increase in biomass after July.

The other species in PM show a very slight growth rate. The highest values are found in different periods of the season, and vary from 0.54 g/m^2/day for *L. vulgare*, 0.54 g/m^2/day for *A. tripolium* and *Su. maritima*, in August-September 1969, and 0.57 g/m^2/day for *Tr. maritima*, in June 1970.

The development in the grazed area of PM is different from that in the enclosures. The highest production rates were found in June (1970) or July (1967-1969); the values are all lower than those of the enclosures (3.20-4.63 g/m^2/day, see table 25). *Puccinellia maritima* has the fastest rate of growth at the beginning of the season, in May or June. The higher values in May and June 1970 are presumably due to the fact that the cattle came into the field later than in the previous years. Even after a period in which no growth was observed (July 1970). partly due to grazing, and probably partly due to a measuring fault during harvesting, which was carried out under very bad weather conditions, the vegetation recovered again and higher rates were reached than in the previous years during the periods of July-August and August-September. The growth rates of *Salicornia* are all lower than in the enclosures. The growth rates also increase here during the season and the maximum values are reached in the July-August period.

CHANGES IN BIOMASS AND FLORISTIC COMPOSITION IN A PLOT OF *PUCCINELLIETUM MARITIMAE* PERMANENTLY REMOVED FROM GRAZING

The results of the harvests from the plot in PM fenced off since April 1968, are given in table 26. After the discontinuation of grazing, an increase can be seen in dead as well as in living material. In September 1971, the weather conditions were very favourable (warm, not much rain and very few storms), so that more living material could be harvested than in the same month in 1970. The total biomasses from September 1970 and 1971 are, however, almost the same. As a result of many years grazing and the consequent manuring, many nutrients were added to the soil. If grazing is discontinued, the vegetation recovers after some time (1968-1969) and the plants are eventually capable of making the best use of the accumulated nutrients (1970-1971). Although harvesting did not take place in 1969, the data in table 26 indicate that the values for the living and dead biomass were presumably between those of 1968 and 1970.

The floristic composition shows a few marked changes over the years. Until 1970 all the species increased in weight except *Sal. europaea* which clearly declined. The germination of *Salicornia*, or its development after germination, is probably impeded in a dense vegetation with a lot of dead material. Much *Salicornia* was present outside the fenced area (see also table 19).

TABLE 26

Changes in biomass and species composition
in a permanent enclosure in grazed *Puccinellietum maritimae*
Values in g/m^2. The percentages of weight of the total living biomass are given in brackets.

Date	25-9-'68	24-9-'69	25-9-'70	20-8-'71	22-9-'71
Treatment	grazed	1 season ungrazed	3 years ungrazed	4 years ungrazed	4 years ungrazed
Total biomass	255	492	780	630	799
Dead material	67	126	332	158	250
Green material	188	366	448	472	549
Puccinellia maritima	86(46)	166(45)	208(46)	83(18)	118(21)
Plantago maritima	19(10)	35(10)	51(11)	109(23)	107(20)
Triglochin maritima	3(2)	2(0.6)	6(1)	28(6)	31(6)
Limonium vulgare	1(0.5)	2(0.5)	51(11)	119(25)	132(24)
Salicornia europaea	62(33)	109(30)	63(14)	25(5)	30(6)
Suaeda maritima	3(2)	14(4)	44(10)	29(6)	49(9)
Spergularia media	6(3)	9(2.5)	22(5)	19(4)	24(4)
Aster tripolium	6(3)	14(4)	3(0.6)	58(12)	56(10)
Other species	2(1)	15(4)	0	2	0

Although the biomasses of *Pucc. maritima* and *Pl. maritima* increased per m^2, their proportion in the total living biomass remained the same in 1968 and 1970 (46% and 10% resp.). The proportion of *L. vulgare* sharply increased from 0.5% to 11%; that of *Su. maritima* also rose from 4% to 10%. With increasing density of the vegetation covering the amount of silt and flood-mark material also increases, which promotes the ecesis of *Su. maritima*. In 1971 a much greater change in the floristic composition can be seen. *Pucc. maritima* declined sharply from 46% to 22% of the total; and *Sal. europaea* from 14% to 5% of the total living biomass. *Pl. maritima, L. vulgare* and *Tr. maritima* increased and now constitute 20%, 24% and 6% respectively of the living biomass. *Limonium* flowered profusely in 1970 and 1971 and *Plantago* in 1971. The biomasses of *Sp. media* and *Su. maritima* remained the same. The development of *A. tripolium* fluctuated. In 1970 very little *Aster* was present; this was also the case elsewhere in the field, and in addition there was general damage to the plants presumably by rabbits and birds (geese and ducks). In 1971 *A. tripolium* developed well; large plants were also found elsewhere in the field. There was also less damage to the plants. The great increase of *Pl. maritima, L. vulgare* and also of *Tr. maritima* and *A. tripolium*, indicates that the vegetation, without grazing, develops into a *Plantagini-Limonietum* stand. This association is present all over the area outside the grazed part; its production is discussed elsewhere in this chapter.

A well developed *Juncus gerardii* stand has grown on a somewhat higher part of ± 2 m^2 in the enclosure. This species is also present in other parts of the biotope (PM) adjacent to the more highly situated drier vegetations. Sampling, in September 1971, of 2 X 1/8 m^2 in this *Juncus* field, gave a standing crop of 811 g/m^2 (363 g/m^2 dead material and 448 g/m^2 living); 25% of the living material consisted of *J. gerardii.*

EXPERIMENT WITH THE MOVABLE CAGES

Although only a small number of samples (8) were taken per harvest date, and although they only had a small surface area (1/8 m^2), there are still a few conspicuous differences in the development of the vegetation, between permanent grazing and alternate grazing/non-grazing (see table 27). After one month of grazing the amount of living material is only slightly less than in the ungrazed plots. After two months of grazing there is a noticeable fall in the amount of dead as well as living material. The fall in the living material is due to consumption; the decrease in dead material cannot easily be explained, but it is probably due to the mixing of material with mud by trampling and thereby being partly lost during harvesting. After 1 month of grazing, followed by 1 month without grazing (cage) there is an increase of living material (33 g/m^2). After 2 months of grazing and 1 month without grazing the dead material as well as the living material increases, but the increase is somewhat less than if the grazing had not been interrupted. The greatest increase in living as well as dead material can be seen after 3 months grazing followed by 1 month without grazing.

When the production per period is calculated from the difference in yield in the cages and the yield of the previous harvest during grazing, the total net production reaches 524 g/m^2. Compared with the production of the enclosures (the whole season without grazing, 528 g/m^2), there is hardly any difference. Thus, the growth of the plants under the influence of grazing is not less than in the enclosures. Apparently growth is even stimulated by grazing. Some of the plant parts are lost at an early stage, by trampling, and no longer take part in the growing process. Even so, the production is the same as if there had been no grazing. The question remains whether this was so in the other years. It has already been indicated that 1970 was a favourable year (cattle later in the field, May-June dry months). In the other years the difference in production between the grazed and ungrazed plots was much greater (see table 23) and there was a sharp decrease in growth after July.

TABLE 27

The influence of grazing on the production of *Puccinellietum maritimae*

Date	Grazed			Caged			Net primary production		
	treatment	standing crop*		treatment	standing crop				
		dead	living		dead	living	dead	living	total
11- 5-'70	first harvest before grazing	63	67						
25- 5-'70	start of grazing								
29- 6-'70	1 month grazed	70	274	1 month ungrazed	70	296	7	296	303
27- 7-'70	2 months grazed	53	247	1 month grazed 1 month caged	69	307	0	33	33
24- 8-'70	3 months grazed	76	283	2 months grazed 1 month caged	70	268	17	21	38
21- 9-'70	4 months grazed	128	342	3 months grazed 1 month caged	136	373	60	90	150
26-10-'70	5 months grazed	–	–	4 months grazed 1 month caged	169	108	–	–	–
							total		524

* values taken from table 19

Results of the crop analyses are given in table 28.

TABLE 28
Crude ash, crude protein and crude fibre content of living material from three salt-marsh communities (Values in percentage per kg dry matter)

Site	Date	Ash	Crude protein	Crude fibre
Junco-Caricetum extensae subass. blysmetosum rufi	24- 4-'67	12.3	10.8	19.8
	22- 6-'67	14.0	9.9	22.1
	16- 8-'67	15.0	9.1	19.7
	16-10-'67	15.7	9.0	22.8
average		14.2	9.7	21.1
	17- 4-'68	38.0	8.4	12.8
	10- 6-'68	11.5	11.1	18.4
	5- 8-'68	11.4	8.2	20.4
	16-10-'68	8.0	9.7	25.2
average		17.2	9.3	19.2
Plantagini-Limonietum	24- 4-'68	31.6	13.6	8.8
	17- 6-'68	21.1	10.4	12.6
	12- 8-'68	22.0	7.3	14.9
	7-10-'68	17.6	10.6	16.6
average		23.1	10.4	13.2
Puccinellium maritimae	30- 5-'67	12.7	15.7	14.8
	24- 7-'67	15.4	8.5	15.1
	19- 9-'67	14.8	8.9	15.2
average		14.2	11.0	15.0
	6- 5-'68	19.9	18.2	9.8
	1- 7-'68	14.1	10.1	13.8
	27- 8-'68	17.4	8.9	15.2
	23-10-'68	13.7	13.3	15.5
average		16.2	12.6	14.6

Crude ash

Large fluctuations were found in the crude ash content of the green plant parts. The highest average was found in the PL material (23% per kg dry material). The average ash contents of the JC and PM material were about the same (14%-17%). These determinations are the averages of the measurements from material taken over the whole vegetation season, in which the floristic composition varies uniformly with the phenological development of the differ-

ent plant species. Analyses of each species in the season will be seen to give different fluctuations. The material of JC in April 1967 consisted of a great deal of *Juncus gerardii* and *Carex extensa* (see table 10), and in April 1968 it consisted mainly of *Plantago maritima*. A marked difference in the ash content is found (12% in April 1967 compared with 38% in April 1968), which indicates that *Plantago* probably has a high ash content. This is also shown from the determinations of the PL material.

There is a tendency towards a decrease in the ash content in all three experimental plots in the course of the season. The ash content gives an impression of the mineral composition of the plant material. The ash probably consists mainly of Si, Ca and Na.

Crude protein

Apart from JC there are also large fluctuations in the protein content during the season. There is a clear decrease from spring to summer; the lowest values are always found in August. From then onwards an increase in the content can again be seen, when fruit has set and many nutrients are transported to the roots. PM presents the highest average value (11.8%) and is followed by PL with 10.4%; JC shows the lowest protein content with 9.5%. The crude protein content is a rough measurement of the nutritional value of the crop.

Crude fibre

Average high percentages are found in JC (20%); in PM and PL the averages were 15% and 13% respectively. There is a rise in the crude fibre content from spring to autumn in the material of all three biotopes. In PL there is twice as much cellulose present in autumn as in spring. This is connected with the ageing of the plant parts. During the season, after seed ripening, much lignocellulose is formed and the plant parts become more woody, as for example the flowering stalks of *Limonium* (in PL) and the stems of *Salicornia* (in PM). The difference in percentage of the JC material in spring is presumably due to the difference in floristic composition (see also ash content).

The cellulose content of the plant plays a role in the decomposition rate of the material by micro-organisms. The fleshy spring material, having a low cellulose content, will break down more quickly than the hard, woody parts of the autumn. These parts are often present for long periods of time in the field (see also Chapter V).

The results of the investigations into the changes in standing crop of some salt-marsh communities show that each biotope exhibits its own specific pattern of development as far as dead and living material are concerned. The amount of dead material is dependent upon the production of the previous year, the mortality during the growing season and the rate of decomposition. In *Puccinellietum maritimae* the extent of grazing also plays a part in the dynamics of the dead material. On the one hand, grazing results in a decrease of the living material; on the other, trampling speeds up the rate of mortality. The removal of dead material by the winter flood-water will be discussed elsewhere. During the four years of investigations the development of the living material was similar per biotope from year to year. The curves for the living biomass also show great similarity when the three experimental plots are compared with each other (figs.9, 11 and 13). From April onwards there is an almost linear increase of green material until a maximum is reached in July and August, followed by a rapid decrease. The period in which green material is present is surprisingly short. Harvesting could not take place at the beginning of April, not only because of the often bad condition of the sites, but also because there was hardly any living material present. The green parts die off in the autumn within a few weeks. The length of this dying off period is dependent upon weather and site conditions, namely inundation.

The three biotopes are characterized by a small number of species. Due to extreme environmental conditions, the salt-marshes belong to the poorest grasslands as far as the number of species is concerned. It should be pointed out here that *Plantagini-Limonietum* is not really grassland in the strict sense of the word because it is not dominated by grasses or grass-like plants. Though many species are common to the three biotopes the preference of any species for an appropriate habitat is shown by its proportion in the production of the total living biomass. Table 29 gives the proportion of a number of species in the production in the month in which the maximum living biomass was harvested.

The living material consists mainly of only 2 or 3 dominant species which together constitute ± 90% of the biomass (see tables 10, 14 and 19). The maximum in living material is therefore also determined by the maximum of one or more of these most important species. The maximum biomass of these species which regularly occur in the samples, generally coincides with their phenological stage of flowering and fruit setting. In this period the flowering stalks play an important part in the biomass, while the mortality of the leaf is already increasing (tables 16 and 17). This all points to the fact that in this period the materials formed previously by assimilation, are for the most part converted into reserve constituents required for reproduction. After this peak

TABLE 29

Distribution of the most important species in the different communities in the month of maximum living biomass in 1970 (in weight percentages of the total living biomass; + indicates less than 0.5%)

	JC	PL	PM
Juncus gerardii	64	1.5	–
Scirpus rufus	2.0	–	–
Carex extensa	1.0	0.5	–
Plantago maritima	23	52	12
Limonium vulgare	+	33	2.5
Triglochin maritima	5	4.5	2
Puccinellia maritima	+	1	40
Salicornia europaea	+	0.5	35
Suaeda maritima	–	–	3
Aster tripolium	+	3	1.0

assimilation still goes on, but degeneration of the plant tissues has already started. A decrease in chlorophyll content can be observed in the field, namely in *Juncus gerardii* and *Limonium vulgare*. An exception is found in *Puccinellia maritima* in PM, which did not flower, presumably as a result of grazing, and in *Plantago maritima* which, due to unexplained circumstances, scarcely flowered at all in PL in 1970.

Until now not a great deal has been published about the proportion of the various species in the living biomass of a community. Only recently, through the IBP, is more attention being paid in this direction. The results of the present research agree with those of Blaisdell (1958), Bray et al. (1959), Pearson (1965), Traczyk (1968, 1971), Kelly et al. (1969). The total number of species in the communities investigated by these authors was, however, much higher, due to which the two most dominant species only constituted 50-60% of the standing crop.

The differences in development and composition in *Puccinellietum maritimae* within the vegetation cages (ungrazed) and outside them (grazed) are small, because due to the annual re-arrangement of the cages the vegetation is only ungrazed for one season. There is a tendency for the maximum in biomass of the species to be reached later in the cages because, in contrast to outside the cages, the plants can grow undisturbed and follow their normal development pattern. As a result of this, the plants in the cages usually flower more profusely.

A relative, although limited decrease of *Puccinellia maritima* is observed in the cages (average 5%, see table 19) compared with outside. After a longer period without grazing the biomass of *Puccinellia maritima* decreases in an absolute sense, as does *Salicornia europaea*, whereas *Plantago maritima* and *Limonium*

vulgare greatly increase. The community probably develops into *Plantagini-Limonietum*, as is suggested by observation in the plot which has been fenced since 1968 (see table 26). It may be concluded that the habitat difference between PM and PL is mainly of a biotic nature, although a number of abiotic factors also contribute to this difference (see the site description and the chapter on abiotic factors).

Westhoff (1951), Westhoff et al. (1970), Chapman (1960), Ranwell (1961) and Beeftink (1965) also mentioned that the biomass of *Puccinellia maritima* greatly increases with grazing. This is apparently mainly due to the decrease of competition from other species, but moreover, it may be that the growth rate of *Pucc. maritima* is directly stimulated by the grazing effect. Contrary to this *Plantago maritima*, *Aster tripolium* and *Triglochin maritima* can only moderately tolerate this grazing and *Limonium vulgare* finally even disappears. The large amount of *Salicornia europaea*, as seen in PM, indicates over-grazing (Beeftink, 1965). Investigations carried out by Van der Zijpp (1971) concerning the activity of the cattle on 'de Groede' have, however, established that the animals had no preference for PM. These observations were, however, limited in number and were only carried out in July and August, while it is possible that in spring and summer more cattle are present in PM and cause relatively more damage due to the site being wet.

After the discontinuation of grazing it is to be expected that the number of species increases gradually. An average of 11 species per 0.125 m^2 was found in PM; in PL an average of 16 species per 0.125 m^2. Ranwell (1961) also recorded an increase in the number of species after the discontinuation of grazing. This seems to be in variance with Westhoff (1969), who, in a succession study of permanent quadrats in *Juncetum gerardii* found a decrease in the number of species after the vegetation had been excluded from the effects of grazing. Westhoff's research, however, extended over a long period of time (30 years) and the investigated biotope was situated inside the dikes, so that there was no inundation by sea-water. This absence of inundation may have resulted in the decrease in the number of species, by the accumulation of litter. In tidal salt-marshes the accumulating litter is periodically removed by the sea.

The vegetation records of 1966 and 1971 (table 1), the data concerning the biomasses of the separate species (tables 10, 14 and 19) and those concerning the occurrence of the taxa (tables 13, 18 and 20) together give an impression of whether there is a certain degree of stability, or alternatively succession, within the investigated vegetation types. Relevant conclusions cannot be drawn about vegetation dynamics from the biomass data alone because the vegetation cages were never placed completely at random.

In PM, no marked changes are indicated during the course of the investigations. Grazing impedes further succession (cf. the permanently ungrazed plot,

where succession does occur). In PL, however, several remarkable changes can be seen; they are especially evident in the records and frequency table (table 18). These changes concern the increase in coverage of *Plantago maritima* and *Festuca rubra*, the increase in occurrence of *Artemisia maritima* (mainly seedlings), and the decrease in coverage of *Carex extensa*. These changes indicate a development towards *Artemisietum maritimae*, an association which lies between the alliances *Puccinellion maritimae* (to which PL and PM belong) and *Armerion maritimae* (to which JC belongs) (see Westhoff & Den Held, 1969). As a result of the silt accretion which, as mentioned in Chapter III, can amount to 3.9-5.0 mm annually a gradual rise in the level of the substrate and a decrease in the frequency of inundation take place.

In JC also important changes took place. The increase of *Juncus gerardii* and the almost complete disappearance of *Scirpus rufus* is striking. The records show that *Agrostis stolonifera* has also increased. Silt was also deposited in this biotope over the last 5-6 years although only to a limited extent. This resulted in a development towards *Juncetum gerardii* (see Westhoff & Den Held, 1969). The frequent sampling by investigators (trampling) of JC, trampling by tourists (JC is situated close to the main path) and also the fact that in 1969 a heavy car drove through the experimental plot, resulting in a change in drainage possibilities for the water, have presumably accelerated the alterations in this biotope. *Junco-Caricetum extensae* subass. *blysmetosum rufi* cannot tolerate grazing, or in this case trampling. The appearance of species such as *Agrostis stolonifera, Leontodon autumnalis, Potentilla anserina* and *Trifolium fragiferum*, species of the alliance *Agropyro-Rumicion crispi* (Westhoff & Den Held, 1969) may indicate this disturbance. However, the appearance of these species may partly be due to the infiltration of fresh-water from the surrounding dunes (Beeftink, 1965; Westhoff & Van Leeuwen, 1966).

Three methods of calculation were applied in order to obtain an impression of the total net primary production from the changes in standing crop. The results of these calculations indicate that the most accurate estimation of the total net production is given when the changes in dead material are also included. This method of production determination is not usually applied; the maximum standing crop of the living material or the sum of the maxima of the separate taxa are normally used to calculate the total net production. The dates given in table 23 show the discrepancies between the results of the different methods. The mortality of the living material and the decomposition of the dead material, in relation to the production determinations, will be discussed more thoroughly in Chapter V.

The annual production of *Plantagini-Limonietum* and ungrazed *Puccinellietum maritimae* (in the enclosures) amounted to an average of ±500 g/m^2; of *Junco-Caricetum extensae* subass. *blysmetosum rufi* and grazed *Puccinellietum*

maritimae (outside the enclosures) the average was ± 350 g/m^2. Experiments with the movable cages in PM showed that growth was probably stimulated by grazing and that also a total production of ± 500 g/m^2 can be reached. The difference in production between grazed and ungrazed vegetation (i.e. 30%) is not unusual. Welch & Rawes (1965; Rawes & Welch, 1966) found that the production of a grazed *Festuca-Agrostis* vegetation was 10%-40% lower than when there was no grazing. Pearson (1965) found a difference in production of 45%, whereby ungrazed was also higher than grazed.

If the difference in net production of the three associations is compared with the difference in soil composition (table 6), a clear relationship is evident. The silt content and the amounts of investigated nutrients in the top layer of the soil are all lower in JC than in PL and PM. The production of JC is considerably lower than that of PL and PM. The difference in the amount of nutrients between PL and PM (PM is richer in nutrients than PL) is only evident when PM remains ungrazed for a few years. In the permanently fenced experimental plot of PM the maximum standing crop of green material was 550 g/m^2 in 1971 (table 26). After a recovery period the vegetation can make optimum use of the nutrients available (cf. also Odum, 1960).

In contrast to this, it is difficult to correlate the annual differences in total production for each biotope separately with the known meteorological and edaphic data for these years (see Chapter III) because, especially as far as the soil is concerned, the measurements carried out during the years of investigations did not always suffice. The influence of weather and/or site conditions on the vegetation as a whole or on a few taxa, during short periods of the growing season, has already been mentioned when discussing the results. A favourable or detrimental temporary influence on the production, does not necessarily have an effect on the total production. The production calculations taken from the sum of the maximum values of the separate species (column 4, table 23), however, show that the annual differences in total production often depend upon fluctuations in biomass of a single species. Only in PM (outside the enclosures) is a clearer relationship evident between the total production and the indirect effect of some abiotic factors. Whenever the area is wet, the vegetation is more vulnerable to trampling than during dry periods. In 1967 for example, the production both inside and outside the cages was low due to the previous very wet summer with much rain and flooding.

Finally, it must be noted that the annual differences in production may be connected with the forementioned changes in the vegetation resulting from succession. Odum (1960) and Golley & Gentry (1965) for example found large differences in annual production, dependent upon the stage of succession of the vegetation.

Neither the consumption of plant parts by animals nor the loss of material

due to plant diseases, were taken into account when the determinations of the net production were made. Very few species of herbivorous mammals are found on the Boschplaat. The wild rabbit (*Oryctolagus cuniculus* L.) and the long-tailed field-mouse (*Apodemus sylvaticus* L.) are numerous; the common shrew (*Sorex araneus* L.) is not very prevalent while the pigmy shrew (*Sorex minutus* L.) is only found very occasionally (Van Mourik, 1968). Grazing by rabbits was eliminated by the vegetatio cages. Outside the cages, damage by rabbits was observed in JC and, to a lesser degree, in PM. Seed consumption by the long-tailed field-mouse is not unlikely in JC, but will only play a very small part in the calculations of the primary production. During the years of the investigations, the long-tailed field-mouse populations, as well as the populations of the shrews, were small and there was enough food for them in the dunes where they have their nests, and in the flood-mark material which is deposited at the foot of the dunes in winter (Van Mourik, personal communication). Only in PM outside the cages must, besides consumption by cattle, also damage by birds be taken into account. In late summer and autumn, flocks of grey lag geese (*Anser anser* L.) are often present in PM which feed on the plants. Research is being carried out to investigate how much these geese influence the production. In JC and PL invertebrates are probably the most important consumers. Damage by *Chrysomelidae* to *Triglochin maritima* and *Plantago maritima*, and the resulting influence on the primary production, was studied by De Smidt (1972). The total loss of material by consumption is probably very small and can be estimated to be less than 5%.

Infections caused by fungi were often found on the plants and clearly caused some damage. *Limonium vulgare* for example was sometimes seriously infected by *Erysiphe communis* (Wallr.) Link and *Uromyces limonii* (Lév.) DC; *Erysiphe sordida* (Jun.) was found on *Plantago maritima* and *Uromyces salicornia* (De Bary) DC on *Salicornia europaea.* In 1970 high mortality of *Salicornia* plants was recorded locally, elsewhere on the Boschplaat, as a result of the latter infection. Boorman (1971) noted that a low production of flowering stalks coincided with a high degree of infection by *Uromyces limonii* in *Limonium vulgare.*

Various authors have compared their production data with those of others. It is of little interest to sum up all the known production values of grasslands and other vegetations. The reader is referred to tables given by Lieth (1962) concerning all production data from natural vegetations as well as from culture crops up to 1960. Reference should also be made to the tables in Odum (1959, 1971), Kelly et al. (1969) and Kosonen (1969). The production of JC, PL and PM is not noticeable high or low compared with the values quoted by these authors. Care should be taken, however, when drawing conclusions from production differences, because the mutually compared magnitudes are not always

equivalent; for example maximum standing crop versus the sum of the maximum values of the species or air-dry weight versus oven-dry weight. It is of interest, however, to compare the production figures found during this research with those of other salt-marsh communities. Many biomass determinations have been carried out in *Spartina* stands. These communities are situated in a zone on the average high-water level and are therefore frequently flooded. Harper (1918 in Lieth, 1962) states a production of 980 g/m^2 in a *Spartina patens* stand. Odum & Smalley (1957 in Lieth, 1962) mention 3300 g/m^2, for a similar vegetation (*Sp. alterniflora* and *Sp. patens*) one of the highest production figures known for natural vegetations. Smalley (1959) found that the maximum standing crop of *Sp. alterniflora* amounted to 970 g/m^2. Maximum standing crops of 710-1060 g/m^2 (air-dry weight) were found by Ranwell (1961, 1964a) for ungrazed *Sp. townsendii* and *Sp. townsendii-Atriplex hastata* communities; for similar grazed areas this was 560-800 g/m^2. Air-dry weights can, however, be 5%-20% higher than oven-dry weights. A total net production (sum of the maximum values of the different species) of ± 850 g/m^2 was measured by Ketner (1970, not published) in a *Sp. townsendii* stand.

Research being carried out by the Institute for Biological and Chemical Research on Agricultural Crops in Wageningen, within the framework of the IBP/PP section (Production Processes), shows that the production, calculated from the sum of the increase in living material with time, of a *Festica rubra* f. *litoralis* stand on Terschelling, amounted to 450 g/m^2. The experimental plot was situated at the foot of the old Stuifdijk at an altitude of ± 135 cm + N.A.P. and was flooded occasionally during high-tides, but more frequently than JC. In similar vegetations, on the island of Schiermonnikoog, the maximum standing crop was 280 g/m^2 in a plot grazed by rabbits and 425 g/m^2 in the ungrazed plot. For further details of this research readers are referred to Alberda (1968-1971).

The high production in the *Spartina* vegetations is probably related to the high frequency of flooding and the regular supply of nutrient-rich silt as a result of this flooding. Ranwell (1964b) found a sedimentation rate of up to 10 cm/year or 500 m^3/ha/year in *Spartina* plots. A comparable amount of silt contains the following amounts of essential nutrients: 800 kg/ha N, 250 kg/ha P and 6500 kg/ha K. According to Ranwell (1964b) there can be absolutely no limitation of growth due to a shortage of nutrients. A decrease in production, however, is noted with a decrease in flooding frequency; compare: *Spartina* biotopes (± 1000 g/m^2), *Plantagini-Limonietum* (± 500 g/m^2), community of *Festuca rubra* f. *litoralis* (± 450 g/m^2) and *Junco-Caricatum extensae* subass. *blysmetosum rufi* (350 g/m^2) (see table 7 for flooding frequencies of JC, PL and PM). After fertilising with N, P and K 900-1000 g/m^2 living material could be harvested in the *Festuca* vegetations of Schiermonnikoog (Alberda, 1970).

These results agree with the hypothesis brought forward by Feekes (1936), stating that the available nitrogen content acts as a limiting factor in salt-marsh ecosystems as soon as the flooding frequency decreases. A relationship between the net primary production and the silt content of the soil was also recorded by Odum (1960). The annual net production measured by this author did not differ greatly on the various soil types, as long as the water and nutrient holding silt-clay fraction was greater than 20%; below 15% the productivity was markedly reduced.

The production of salt-marsh communities is presumably influenced not only by the available nutrients but also by the salinity of the soil. Laboratory experiments into the photosynthetic capacity and relative growth rate (g/g/day) of some halophytes, have shown that these parameters for e.g. *Festuca rubra* f. *litoralis* and *Plantago maritima* are almost the same as for the high-producing species of grasses such as *Lolium perenne*. The annual production of the latter species can amount to 2000 g/m^2 (Alberda, 1968).

It is difficult to compare the production rates of various vegetation types with each other, because the lengths of the periods over which they are calculated often differ. Very high production rates can often be calculated over short periods, while they can be lower when taken over longer periods of time. For example, the rate of production for the period April 16th - May 14th was 4.24 g/m^2/day for JC in 1969, while in the period May 2nd - May 14th it amounted to 6.38 g/m^2/day (see table 25). Golley & Gentry (1965) found, in a herb vegetation, productions of 2.25, 3.06, 5.14, 1.35 and 1.91 g/m^2/day for the months of April, May, June, July and August respectively. In an *Arrhenatheretum*, Jankowska (1967) found a production rate of 6.8 g/m^2/day in May and 6.3 g/m^2/day in September. Kelly et al. (1969) mentioned productions of 1.21, 3.20, 1.66 and 1.38 g/m^2/day for a *Festuca elatior* vegetation for the periods March 1st - April 28th, April 28th - May 15th, June 19th - July 24th and July 24th - September 26th respectively. Just as in the present research the highest values were always found in May-July.

Because of the short period in which production takes place, the studied salt-marsh communities differ greatly from communities in which green shoots are always present. For almost six months salt-marsh communities are in an inactive condition; no photosynthesis is possible then. Because of this short growing season the production rate for the separate periods is often higher than for comparable periods of time in other communities. The production rate calculated over the total growing season can, however, be similar to that of other communities. The average value for JC, PL and PM of 2-3 g/m^2/day for a growing season of six months is similar to that of prairy communities and to the world average of wheat, maize and oats, calculated over the same interval of time (Odum, 1959).

The chemical analyses are too scanty to be entered into in detail. Closer investigation into the mineral composition of salt-marsh plants is being carried out in co-operation with the Institute for Biological and Chemical Research on Agricultural Crops in Wageningen. The results of this research will be published elsewhere. The crude ash contents given in table 28 are high, compared with the results of analyses quoted by other authors (Jankowska, 1967; Boyd, 1970; Jakrlová, 1971). According to Wetzel (1966) the high mineral content of the plants is one of the factors which make the salt-marshes good quality pasture-land. The way in which the crude protein content was determined, namely by multiplying the total amount of N present in the plant material by a factor of 6.25, is disputable (Voison, 1961) and the result gives little information about the true amounts of protein in the plants. There is still very little known about the content of crude protein and crude fibre in wild plants.

THE DECOMPOSITION OF DEAD PLANT MATERIAL

Method

Experiments into the decomposition of dead plant parts were carried out in close connection with the determination of the changes in standing crop and with the production calculations as discussed in Chapter IV. Two different methods were applied.

The first method is the paired-plot method as described by Wiegert & Evans (1964). This method was modified and simplified by Łomnicki & Bandoła (1967), Łomnicki, Bandoła & Jankowska (1968) and again simplified by Jankowska (1968). This last modification is used in the experiments and will be referred to as the Wiegert-Evans method. The procedure was as follows: at the start of the growing season (end of April - beginning of May) a circular experimental plot of 0.125 m^2 was chosen and marked out in each vegetation cage. From each of these experimental plots, the 'model plots', all the dead material was removed very carefully so as not to damage the green plant parts. At intervals of four weeks, the dead plant parts (h) which had arisen due to the mortality of the green material, were removed from these model plots. At the same time all the plant material was removed from a plot of the same size, ± 30 cm away from the model plot, having a similar floristic composition and coverage as the model plot. This material was separated in the laboratory into dead (g) and living (b).

From the amount of dead material present at the beginning and end of a period the rate of decomposition of dead material can be calculated by using the formula (see for details Wiegert & Evans, 1964; Łomnicki, Bandoła & Jankowska, 1968):

$$r = \frac{\ln W_0/W_1}{t_1 - t_0}$$

where

r = rate of decomposition of dead material in g/g per day

W_0 = amount of dead material (in gms) at t_0

W_1 = amount of dead material (in gms) at t_1, in as far as it was already

present at the beginning of the period (that is to say, no dead material is added during the time interval $t_1 - t_0$)

$t_1 - t_0$ = time interval in days

The value W_1 was obtained from the values found for g and h. The amount of dead material g at t_1 is the amount of material at t_0 plus the dead material produced in the period $t_1 - t_0$ minus the dead material which decomposes during this time interval or:

$$g = W_0 + h - (W_0 - W_1) \text{ or } W_1 = g - h.$$

It is assumed here that the rate of decomposition of both plots (that for the determination of W_0 and that for W_1) are the same per interval of time. The measurements of the amount of dead material of the model plots, at the beginning of the experiment, are the W_0 values for the first period. The values for g at the end of a period were used as W_0 for the following period.

From the values r_i for each of the paired plots the arithmetic mean r_i was calculated for the respective periods (cf. Łomnicki & Bandoła, 1967; Jankowska, 1968).

The amount of dead material which decays per time interval is given as x_i, this is thus $W_0 - W_1$.

The data concerning the amounts of dead and living biomass, collected each month from the small plots close to the model plots, were also used for the determination of changes in standing crop and floristic composition, as described in the previous chapter.

The values for h_i, which are a measure of mortality of the living material, were at the same time used to calculate the increase in green (living) material (net primary production = y_i per time interval), by using the formula according to Wiegert & Evans (1964),

$$y = h + (b_1 - b_0)$$

in which h is the same as parameter d used by Wiegert & Evans, and b_1 and b_0 are the standing crops of green material at the end and beginning of the time interval respectively. The sum of the y_i-values is a measure for the total net primary production of the growing season under consideration (cf. also Chapter IV).

Two assumptions were made when determining the mortality (h) and the increase in green material, in the manner described above, namely that the death rate of the green material in the model plots was not influenced by the presence or absence of dead material, and secondly that none of the dead material decomposed during the time interval in which it was formed (Łomnicki, Bandoła & Jankowska, 1968). It should be noted here that the first assumption also applies for a correct determination of W_1.

The Wiegert-Evans experiment was carried out in 1968 and 1969 in JC and PL. In 1968 5 model plots were set out in JC and 10 in PL. In 1969 10 model plots were chosen in both vegetations; one in each vegetation cage. The time interval between the collection of the newly-formed dead material was about 4 weeks in 1968; in 1969 the dead material was collected every fortnight from the model plots from August onwards. The total amount of newly-formed, dead parts over an interval of 4 weeks, was calculated by adding together the fortnightly values ($h_1 - h_2$). In October all the material (dead and living) was collected from the model plots and separated into dead and living parts in the laboratory. This is carried out in order to remove the chance of errors made during the collection of dead material in the field due to very bad site conditions.

The rate of decomposition for the period April-May was calculated from the amount of dead material present at the beginning and end of the period respectively, whereby it was assumed that there was no mortality of green parts during this time interval.

The values for y_i for the period April-May are the differences in yield at the end and beginning of this period. It can be expected that mortality of green parts has not yet started in this period. It was also assumed that there is no green material present during the winter (cf. Chapter IV, production calculations).

A second, much simpler, method which was applied to determine the rate of decomposition is the litter-bag technique (Shanks & Olson, 1961; Wiegert & Evans, 1964; Jakrlová, 1967). This method has only been applied in JC and was used there in 1968 and 1970. The method is as follows: in spring bags made from a Dralon net curtain were filled with a known amount of dead plant material and placed in the field on spots representative of the whole studied vegetation. The vegetation was completely removed from the spots and the bags placed on the uncovered soil; they were fastened with pegs to prevent them from being blown away or from being carried away by flood-water.

In 1968 each bag (measuring 16 X 12 cm) having a mesh width of 3 mm^2 on the lower side and 9 mm^2 on the upper side, contained 15 g dry weight of dead material. In 1970 each bag (measuring 18 X 14 cm) was filled with 10 g dry weight plant parts, and the mesh widths were 2.2 mm^2 on both sides. In 1968 the bags were placed in groups scattered over the whole experimental plot; in 1970 a field of 15 X 10 m was chosen in which the bags were placed in rows with distances of 20 cm between them.

At intervals of 4–6 weeks five bags, chosen at random, were taken from the field. The time intervals were longer during winter. Sand and shoots, which had grown through the meshes, were removed and the dead material was dried at a temperature of 85°C and then weighed. Values for the rate of decomposition r could be calculated from the average amount of dead material present at the

beginning (= $\overline{W}_0$) and end (= $\overline{W}_1$) of a time interval, using the formula

$$r = \frac{\ln \overline{W}_0/\overline{W}_1}{t_1 - t_0}$$

The average value for $\overline{W}_1$ was always used as $\overline{W}_0$ for the following time interval (cf. Wiegert & Evans, 1964).

The plant material used in the experiment was taken from the harvests of the previous year and had a floristic composition comparable to that of the field.

Sample results

WIEGERT-EVANS METHOD

Junco-Caricetum extensae subass. blysmetosum rufi

The values calculated for r_i, x_i, h_i and y_i in JC are given in table 30 and fig.17. This table also gives the mean values for W_0 and W_1 (average of 5 or 10 samples) with the standard errors (S.E.M.). The rate of decomposition shows large fluctuations in both years. In 1968 low values for r_i were found in the middle of the season, June-July, (–0.003 g/g/day). There is an increase of r_i from July to September followed by a slight decrease until October. Maximum decomposition takes place in spring, April-May harvest period, and in the August-September harvest period. The curve for r_i shows the same tendency in 1969. Similarly, minimum values were found in the middle of the growing season, while maximum decomposition occurred in autumn but one month later than in 1968. During the period April-May 1969 r_i could not be calculated because more dead material was found in May than in April ($W_1 > W_0$). For the period May-October in 1968 the average value for r_i is 0.018 g/g/day and in 1969 0.014 g/g/day.

As can be expected, the curves for x_i (amount of decomposed material) follow the course of those for r_i (see fig.17). At a high rate of decomposition much dead material disappears; at a low rate of decomposition little material disappears, depending, of course, upon the amount of dead material at the beginning of the period under consideration.

The mortality curves are almost the same for both years. The mortality (h_i) increases gradually during the season and reaches a maximum in September-October, when almost all the plant parts die off (cf. also fig.9 in Chapter IV).

The greatest increase in living material (y_i) takes place in the periods May-June and June-July in 1968 and is then 111 g/m^2 and 105 g/m^2 respectively. The values for the same periods in 1969 only differ very slightly from those of 1968 (104 g/m^2 and 108 g/m^2 respectively). After July the increase in living material is much less, especially in 1968.

TABLE 30

Decomposition rates, disappearance, mortality and growth of above-ground plants parts in *Junco-Caricetum extensae* subass. *blysmetosum rufi*

Year	Period	t_1-t_0	n	$\bar{W}_0$	$\bar{W}_1$	$\bar{r}_1$	x_i	h_1	y_i
1968	until 17/4		15	–	–		–	–	60.6
	17/4–16/5	29	15	–	–	0 032 (0.012)**	148.6	–	26.1
	16/5–12/6	27	5	14.7 (2.4)*	11.6 (0.6)	0.007 (0.007)	24.9	5.4	110.9
	12/6–10/7	28	5	12.2 (0.6)	13.2 (0.3)	0.003 (0.002)	0 0	12.9	105.0
	10/7– 7/8	28	5	14.8 (0.3)	10.5 (2.7)	0.017 (0.009)	34.5	31.9	38.6
	7/8– 4/9	28	5	14.5 (2.8)	5.7 (1.5)	0 041 (0.016)	69.9	33.1	21 3
	4/9–16/10	42	5	9.6 (1.5)	4.7 (0.8)	0.017 (0.003)	39.2	83.5	(–66.0)
	total						317.1	166.8	362 5
1969	until 16/4		15	–	–	–	–	-	31.0
	16/4–14/5	28	10	–	–	–	–	–	87.9
	14/5–11/6	28	10	19.8 (1.4)	15.0 (1.3)	0.009 (0.003)	37.7	7.0	104.2
	11/6– 9/7	28	10	15.9 (1.3)	15.9 (1.7)	0 001 (0.006)	0.2	11.8	107.7
	9/7– 6/8	28	10	17.3 (1.6)	15.6 (1.8)	0.004 (0.003)	14.4	38.1	72.1
	6/8– 3/9	28	10(9)	20.3 (2.0)	12.4 (1.4)	0.016 (0.004)	63.7	30.2	0.0
	3/9– 4/10	31	10(9)	16.2 (1.7)	6.7 (2.0)	0.041 (0.010)	76.0	129.7	56 7
	total						192.0	216.8	459.6

* The values between brackets are the standard errors of the mean (S.E.M).

** No paired plots. Value calculated from standing crops of dead material on the two dates.

Explanation of signs

t_1-t_0 = time interval in days, n = number of samples; $\bar{W}_0$ = average amount of dead material at time t_0 in g/0.125 m^2, $\bar{W}_1$ = average amount of dead material at time t_1 in g/0.125 m^2, only that material is considered which was already present at t_0, $\bar{r}_1$ = average decomposition rate of dead material in g/g per day, calculated from the values r_1 for each of the paired plots, x_1 = amount of dead material decayed in time t_1-t_0, h_1 = mortality of green material in time t_1-t_0, y_1 = increment of green material in time t_1-t_0, x_1, h_1 and y_1 are in g/m^2.

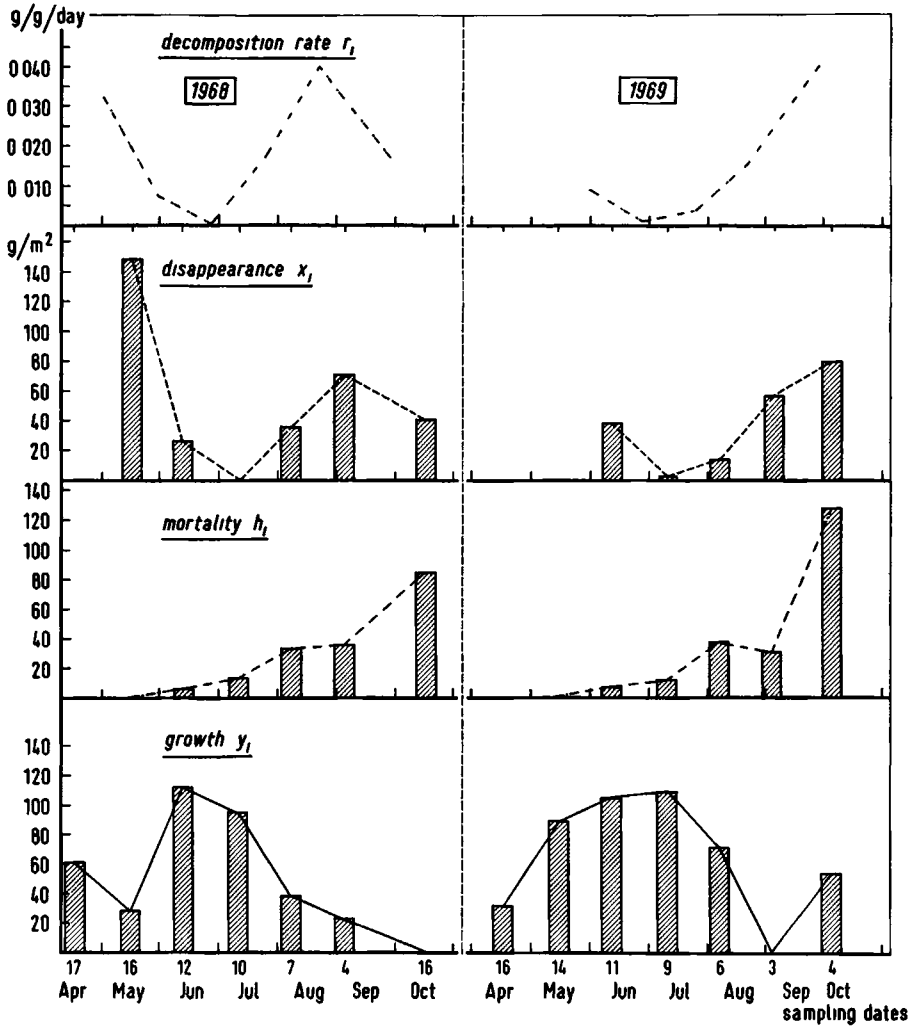

Fig 17 Decomposition rate of dead material (r_1), in g/g/day, measured with the paired-plot method in *Junco Caricetum extensae* subass *blysmetosum rufi*, with disappearance of dead material (x_1), and mortality (h_1) and growth (y_1) of green material in successive months

The crop values x, h and y at the sampling dates, as represented by the histograms, have been connected by a line This line, however, does not allow any interpolation as to intermediate data It only serves to facilitate the comparison of data relating to both years

Plantagini-Limonietum

The results obtained from the calculations of r_1, x_1, h_1 and y_1 for PL are given in table 31 and fig 18. In 1969 no value for r_1 could be calculated for the

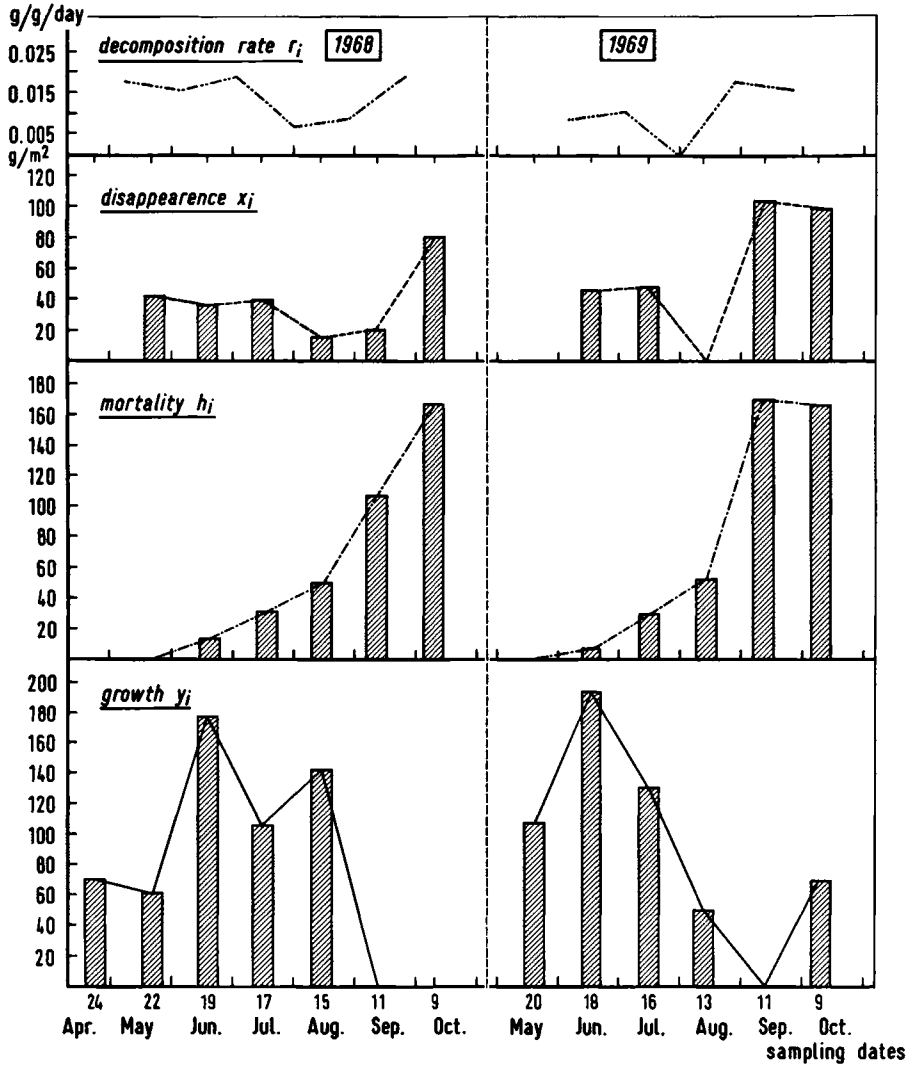

Fig.18. Decomposition rate of dead material (r_i), in g/g/day, measured with the paired-plot method in *Platagini-Limonietum*, with disappearance of dead material (x_i), and mortality (h_i) and growth (y_i) of green material in successive months.

The crop values x, h and y at the sampling dates, as represented by the histograms, have been connected by a line. This line, however, does not allow any interpolation as to intermediate data. It only serves to facilitate the comparison of data relating to both years.

April-May period because more dead material was found in May than in April. In PL, as in JC, the rate of decomposition was found to fluctuate during the

TABLE 31

Decomposition rates, disappearance, mortality and growth of above-ground plant parts in *Plantagini-Limonietum*

Year	Period	t_1-t_0	n	$\overline{W}_0$	$\overline{W}_1$	$\bar{r}_i$	x_i	h_i	y_i
1968	until 24/4		15	–	–	–	–	–	73.8
	24/4–22/5	28	15	–	–	0.018 (0.008)**	42.2	–	63.0
	22/5–19/6	28	10	15.8 (2.7)*	11.1 (2.2)	0.016 (0.009)	37.3	14.1	177.3
	19/6–17/7	28	10	12.8 (2.1)	7.8 (1.5)	0.019 (0.010)	40.0	33.9	106.4
	17/7–15/8	29	10	12.0 (1.7)	10.0 (1.6)	0.007 (0.006)	16.0	50.1	143.4
	15/8–11/9	27	10	16.3 (1.7)	13.9 (2.0)	0.008 (0.008)	19.0	108.4	(–33.3)
	11/9 - 9/10	28	10	27.4 (1.8)	17.3 (2.3)	0.019 (0.007)	80.6	166.4	(–80.6)
	total						235.1	372.9	563.9
1969	until 20/5		15	–	–	–	–	–	105.5
	20/5–18/6	28	10	31.9 (2.4)	25.8 (2.9)	0.009 (0.005)	48.3	6.3	192.3
	18/6–16/7	28	10	26.7 (2.9)	20.6 (2.4)	0.011 (0.006)	49.8	29.7	134.6
	16/7–13/8	28	10	24.3 (2.4)	25.1 (2.4)	0.001 (0.005)	00.0	59.3	50.1
	13/8–11/9	29	10	32.5 (2.4)	18.1 (2.4)	0.018 (0.004)	115.3	169.8	00.0
	11/9– 9/10	28	10	39.3 (2.7)	25.6 (2.8)	0.016 (0.004)	110.2	166.9	70.2
	total						323.6	412.0	552.7

* The values between brackets are the standard errors of the mean (S.E.M.).

** No paired plots. Value calculated from standing crop of dead material on the two dates.

Explanation of signs:

t_1-t_0 = time interval in days; n = number of samples; $\overline{W}_0$ = average amount of dead material at time t_0 in g/0.125 m^2; $\overline{W}_1$ = average amount of dead material at time t_1 in g/0.125 m^2, only that material is considered which was already present at t_0; $\bar{r}_i$ = average decomposition rate of dead material in g/g per day, calculated from the values r_i for each of the paired plots; x_i = amount of dead material decayed in time t_1-t_0; h_i = mortality of green material in time t_1-t_0; y_i = increment of green material in time t_1-t_0; x_i, h_i and y_i are in g/m^2.

vegetation season. In 1968 the lowest values were found in August-September, while June-July and September-October are the periods with a high rate of decomposition. The maximum value obtained is 0.019 g/g/day in the June-July and the September-October period. In 1969 as in 1968 there is a slight rise of r_i in the June-July period (see fig.18), followed by a decrease in the July-August period. The highest rate of decomposition is found in September. Great similarity can also be seen when the curves of r_i for both years are compared, especially for the June-July-August period. In 1969 the maximum is reached one month earlier than in 1968 (September and October resp.). With the exception of the maximum values, all the other values for r_i in 1968 are larger than in 1969. The average values for r_i during the period of investigation, are 0.014 and 0.011 g/g/day in 1968 and 1969 respectively.

The curves for x_i follow the course of those for r_i. Maximum values for x_i are found in September-October, when there is much dead material present and the decomposition rate is greatest.

From May onwards there is a gradual increase in mortality of the green plant parts; as in JC a maximum is reached in autumn.

The greatest increase in living material (y_i) is in the May-June period (177 g/m^2 in 1968 and 192 g/m^2 in 1969). The increase in green material is still large in August 1968 and July 1969 (143 g/m^2 and 136 g/m^2 resp.). After reaching these values the increase in living material becomes less as growth decreases. In September-October 1969, however, a small re-growth is observed (70 g/m^2).

If JC and PL are compared with each other, it can be seen that the values for the rates of decomposition of dead material are not very similar, except that r_i decreases in the middle of summer and that the maximum values are found at the end of the summer and the beginning of autumn. The mortality of the green material (h_i) in JC is less uniform than in PL. The maximum values for r_i, x_i and h_i, in JC as well as in PL in the August-October period, are clearly a result of the fact that almost all the green material dies off during this period and decomposition of the dead material occurs. A maximum increase (production) in living material occurs in both areas in the May-June period. The curves for y_i in JC and PL are rather similar, but the increments in PL are always greater than in JC. In 1969 an increase of green material can be seen again in the September-October period in both sites (see tables 30 and 31). This was not the case in 1968. This re-growth in 1969 followed a period (the last 10 days of August) of very bad weather (a lot of rain and wind), during which PL was flooded several times successively (see table 7) and a great deal of rain-water stagnated in JC. As a result, the mortality of the plants increased, especially in PL, while growth was arrested ($y_i = 0$ in both vegetations). In the subsequent period, when the weather conditions were very favourable (dry, warm with a

great deal of sun; see tables 2 and 5), the vegetation recovered and new, green parts developed. In JC this re-growth consisted mainly of new shoots of *Juncus gerardii, Scirpus rufus* and *Agrostis stolonifera*; in PL of new leaves of *Limonium vulgare* and *Plantago maritima*. The relatively high increase early in the season of 1968 is probably a result of the favourable weather conditions.

Total net primary production

The total net primary production was calculated by adding the y_i values per time interval. The negative values of y_i, found in late summer and autumn were omitted in the calculation. It was assumed that $y_i = 0$ in these time intervals. The production figures (calculated in this way) are given in table 32. For comparison the production calculations for these years, as stated in table 23 of Chapter IV, are also given in this table.

TABLE 32

Net primary production in g/m^2 (dry weight), calculated from the increase in green material, compared with results of production calculations, as given in table 23

	Year	Σy_i	Maximum standing crop	Sum maximum values of the species	$\Sigma(\Delta a+\Delta b)$
JC	1968	363	291	320	291
	1969	460	346	372	395
PL	1968	564	466	486	532
	1969	553	397	424	462

Table 32 shows that the total primary production values defined as Σy_i are much greater than the production figures calculated in other ways. The differences between the maximum standing crop and Σy_i are the most (1968: 25% in JC, 21% in PL; 1969: 33% and 39% resp.). The differences between Σy_i and $\Sigma(\Delta a + \Delta b)$ are rather less (JC 25% and 16%; PL 6% and 20%, in 1968 and 1969 resp.). As was already described, in the production calculation according to $\Sigma(\Delta a + \Delta b)$ the mortality of green material is only partly taken into account.

LITTER BAG EXPERIMENT

The results of this experiment are given in table 33 and fig.19. As with the Wiegert-Evans method, the litter-bag experiment also shows that the rate of decomposition is subject to fluctuations. In 1968 low values for r_i were found in June-July and August-September; the highest value in the September-

TABLE 33

Instantaneous rates of disappearance of dead material from mesh bags in *Junco-Carcetum extensae* subass *blysmetosum rufi*

Year	Interval	t_1-t_0	n	$\overline{W}_0$ (S E M)	n	$\overline{W}_1$ (S E M)	$r_1=\frac{\ln \overline{W}_0/\overline{W}_1}{t_1-t_0}$	S D	x
1968	24/5 –14/6	21	5	15 0 (0 0)	5	13 2 (0 2)	0 006	0 001	12
	14/6 –12/7	28	5	13.2 (0 2)	5	12 4 (0 4)	0 002	0 001	17
	12/7 – 9/8	28	5	12.4 (0 4)	5	9 7 (0 1)	0 009	0 001	35
	9/8 – 5/9	28	5	9 7 (0 1)	5	9 2 (0 5)	0 002	0 002	40
	5/9 – 4/10	28	5	9 2 (0 5)	5	6 4 (0 6)	0.013	0 004	57
	4/10– 1/11	28	5	6.4 (0 6)	5	5 8 (0 4)	0 004	0 004	62
	1/11–29/11	28	5	5 8 (0 4)	5	6 0 (0 3)	–0 002	0 003	62
1970	20/4 –27/5	37	5	10 0 (0 0)	5	7 9 (0 2)	0 006	0 001	21
	27/5 – 8/7	42	5	7 9 (0 2)	5	6 3 (0 3)	0 005	0 001	37
	8/7 –12/8	35	5	6 3 (0 3)	5	5 8 (0 2)	0 003	0 002	44
	12/8 –16/9	35	5	5 8 (0 2)	5	4 0 (0 2)	0 011	0 002	60
	16/9 –23/10	37	5	4 0 (0 2)	5	2 7 (0 3)	0 010	0 004	73
	23/10–25/11	33	5	2.7 (0 3)	6	2 6 (0 2)	0 001	0 004	74
1971	25/11– 2/2	70	6	2.6 (0 2)	5	2 9 (0 2)	–0 002	0 001	74
	2/2 –16/3	42	5	2 9 (0 2)	6	2 9 (0 2)	0 000	0 002	74
	16/3 –14/5	59	6	2 9 (0 2)	10	1 5 (0 2)	0 011	0 002	85
	14/5 –30/6	47	10	1 5 (0 2)	5	1 4 (0 2)	0 001	0 004	89

Explanation of signs

t_1-t_0 = a time interval in days, n = number of samples, $\overline{W}_0$ = average amount of dead material at t_0 in gms, $\overline{W}_1$ = average amount of dead material at t_1 in gms, S E M = standard error of mean, r_1 = instantaneous rate of disappearance in g/g per day, S D = standard deviation (computed by linear approach of the function $f(x,y)=\frac{\ln (x/y)}{t_1-t_0}$), x = amount of decayed material in percentage of initial bulk

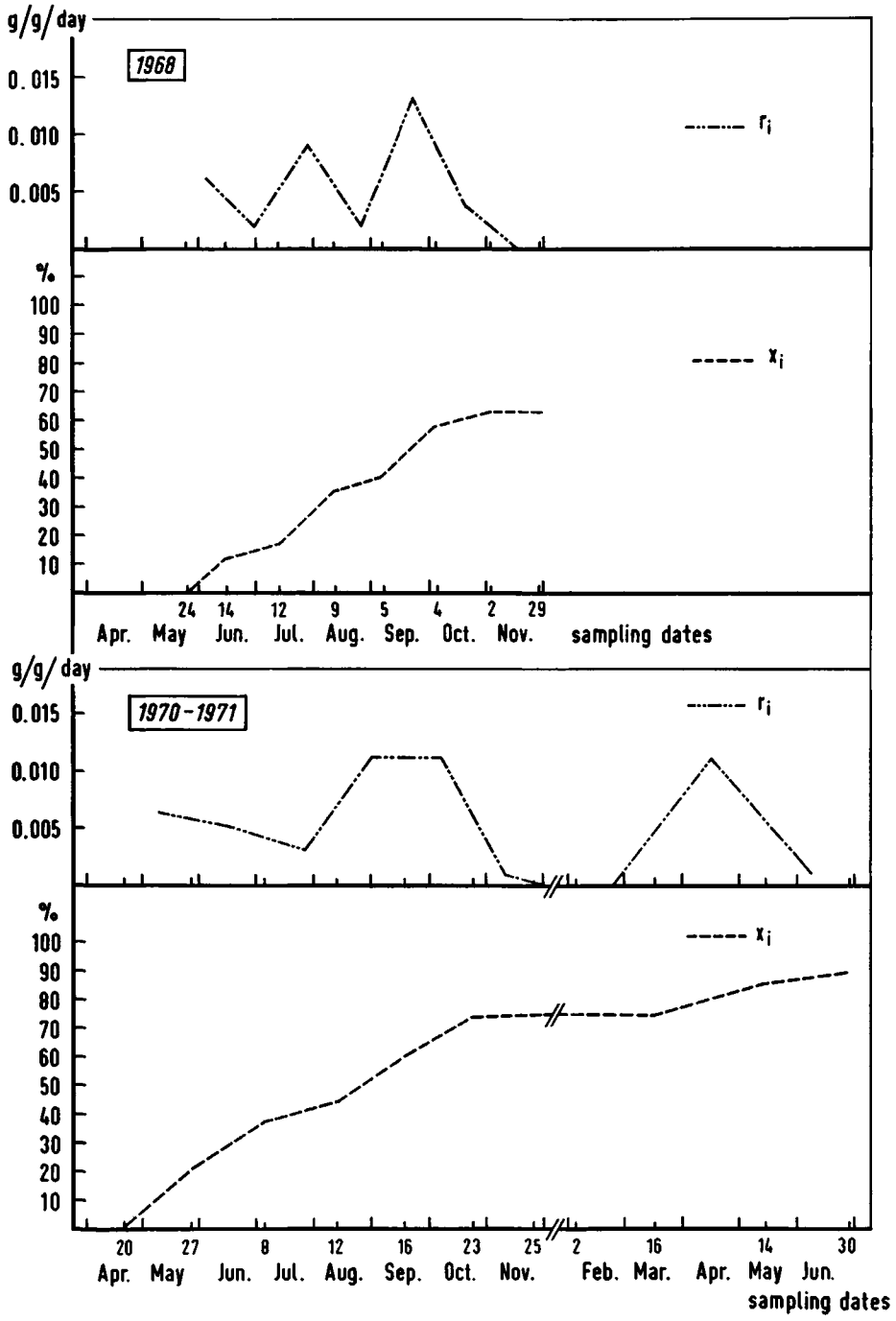

Fig.19. Instantaneous rates of decomposition of dead material from mesh bags in *Junco-Caricetum extensae* subass. *blysmetosum rufi*. r_i = decomposition rate in g/g/day; x_i = amount of decomposed material in percentage of initial bulk.

October period (0.013 g/g/day). After October the rate of decomposition decreases to zero. The fluctuations of r_i are smaller in 1970. A distinction can be made between two periods that year, one from May to August with a low rate of decomposition and one from August to October with a high rate of decomposition. In the second half of autumn and during the winter, no decomposition of dead material occurs. In spring of 1971 a high rate of decomposition was found to have occurred again (0.011 g/g/day).

Bags containing dead material from the 1970 series could not be collected after June 1971 because there was too much sand in them and the plant material which had grown through the meshes could no longer be separated from the original material.

At the end of the 1968 season, 62% of the original material had decomposed; in 1970 this was 74%. In the spring of 1971 a further 15% (of the original 10 g) decomposed; thus, in June 1971, 14 months after the bags had been set out, 89% of the contents had decayed.

When the values for r_i, found with the litter-bag experiment, are compared with those calculated according to the Wiegert-Evans method, little similarity can be seen. The maximum values for r_i in the litter-bag experiment are almost half of the maximum values obtained from the other experiment. The average for r_i of 1968 in the litter-bag experiment is less than half of the average r_i value obtained from the Wiegert-Evans method, calculated over the same period. There is, however, some agreement concerning the periods in which the decomposition rate is high or low (cf. figs.17, 18 and 19). The results from both experiments show that r_i is high in the late summer - early autumn period and low in the middle of the vegetation season.

Neither method, used to study the rate of decomposition of dead plant parts, gives a positive answer about the differences in desintegration of the various species or parts of species in the vegetation. Observations in the field and during the separation of the dead and living material in the laboratory, give more information about this feature. In spring, the dead material of JC consists mainly of the leaves and flowering stalks of *Juncus gerardii, Scirpus rufus, Carex extensa* and *Agrostis stolonifera* from the previous years. The dead *Juncus gerardii* plants of the previous season are still upright. Decomposition begins on the older parts which are lying on the surface of the soil. During the growing season this decomposition continues but newly-formed dead material also decays. Belonging to this category are the succulent plant parts such as e.g. the leaves of *Plantago maritima, Triglochin maritima, Scirpus rufus* and, in the late summer-autumn period, the annual plants such as *Centaurium pulchellum* and *Odontites verna* and especially the leaves of the latter. Only a small part of the *Juncus* material from the previous season takes part in the decomposition process, but the leaves and flowering stalks finally come to lie on the ground

and form a thick layer. When there is an increase in dead material in September, as a result of the rapid dying off of green parts, there are always plant remains still present which are one, two or more years old.

At the beginning of the season, the dead material in PL consists mainly of the leaves and flowering stalks of *Limonium vulgare* of several years old (distinguished by differences in colour) and the leaves of *Plantago maritima*. The latter covers the soil with a thin layer which is very fragile in dry periods. During the growing season almost all the dead leaves of *Plantago maritima* of the previous season disintegrate as well as part of the newly-formed dead material of *Plantago*. Other plant parts, such as the leaves of *Triglochin maritima* and *Aster tripolium*, can also decompose during the same season in which they were formed. Only very few leaves of *Limonium vulgare*, formed in previous years, decay and mainly those which are the oldest and lying closest to the ground. Many *Limonium* leaves are added to this mass of dead material during the growing season.

Although no decomposition takes place in the winter, a great deal of material disappears from PL due to the fact that it is carried along with the flood-water and deposited elsewhere on higher parts as flood-mark material and decomposes there. This flood-mark material usually contains many flowering stalks and leaves of *Limonium vulgare* and *Plantago maritima* and the woody stems of *Salicornia europaea*. A certain amount of material from JC also decomposes, not in the same place where it was formed, but elsewhere as flood-mark material. This amount is much smaller than that of PL, due to the fact that JC is less frequently inundated and the rate of flow of the flood-water in JC is much slower than in PL, and consequently less material is loosened.

Discussion

WIEGERT-EVANS METHOD

Several comments can be made about the formulae used, about the applied analysis technique, and about the interpretation of the results, on the basis of the possible model assumptions.

Because of the large standard errors (S.E.M.) (see tables 30 and 31) the differences per biotope between the r-values for each period are often hardly significant. Large standard errors in the r-values per time interval were also found by Łomnicki & Bandoła (1967). Wiegert & Evans (1964) on the other hand, did not give any standard errors. The most important factors which influence these errors (S.E.M.) are weighing errors, the paired-plot method error and the fact that the rate of decomposition is presumably plot dependent.

In other words the decomposition rate is not the same per time interval over the whole biotope, but differs from place to place depending on the micro-environment.

The results obtained from the litter-bag experiment raise the suspicion that there is a certain degree of plot dependency, at least as far as JC is concerned (see table 34 and elsewhere in the discussion).

It can be concluded from the individual determinations of W_0 and W_1 that a large paired-plot method error is to be expected, whereas the weighing errors are negligent. The average rate of decomposition will, therefore, generally be over-estimated; in the case of large paired-plot method errors, this over-estimation can be considerable. Due to the fact that the actual W_1 determinations may be influenced by a plot dependent decomposition rate as well as by the paired-plot method error, it does not seem to be possible to separate these sources of error without additional information.

From the data obtained with the Wiegert-Evans method (tables 30 and 31; figs.17 and 18), it seems that each community has its own decomposition dynamics, which vary from year to year depending upon environmental conditions. The rate of decomposition for JC seems to be, on average, somewhat higher than for PL, while the values in both biotopes in 1968 are higher than in 1969. The curves for r_i from both communities show a certain similarity over the 2 years of investigations, namely that the decomposition rate is greater in spring and autumn than in the middle of the season.

The decay of dead material can be seen as a clear indication of microbiological activity (Witkamp, 1963; Jacubczyk, 1971). The curves showing the rate of decomposition reflect the variation in the population density and in the metabolic activity of the microflora (fungi, bacteria). Due to the fact that the micro-organisms are subject to definite fluctuations during the season (Witkamp, 1960, 1963; Jacubczyk, 1968, 1969), the decomposition of plant material also fluctuates. These fluctuations are closely related to the environmental variables (edaphic conditions and meteorological factors).

Humidity and temperature seem to be the main factors influencing decomposition in JC and PL. Although the data concerning the ground-water level (fig.6), soil humidity (table 8 and fig.7) and temperature (table 2) strengthen this supposition, it has not been proved experimentally. In the spring of 1968 when the temperatures were higher than normal with favourable conditions of humidity (areas not inundated but swampy), high values were found for r_i. Similar results were found by Witkamp (1963) during investigations into populations of micro-organisms on leaf litter in relation to environmental factors and decomposition. The period of great activity is followed by a period (in the middle of the summer) of limited decomposition. This is presumably a result of the fact that the soil surface dries with the rise in temperature, while there is

only little flooding or rain. Owing to this either the metabolic activity or the number of micro-organisms decreases. The activity of the micro-organisms can also decrease independently of the environmental conditions because the organisms have their own definite rhythm of activity; for example each period of high activity is followed by one of low activity (cf. Jacubczyk, 1970; Witkamp, 1966). In late summer and autumn conditions become more favourable again and decomposition increases. From October-November to the following spring there is no decomposition due to the cold weather conditions and prolonged and frequent inundation of the experimental plots.

The fact that the activity of the micro-organisms depends on fluctuations in the site conditions, may account for the difference in the rate of decomposition in PL compared with JC. The site conditions in PL are much more liable to fluctuations during the season than in JC. During the season PL can be flooded by sea-water and, for short periods (in June and July), it can be dry and then after heavy showers the rain-water can stagnate for a short time. The micro-organisms are continually adapting to the new conditions. The difference in the composition of the dead material also plays an important role in the rate of decomposition (see also Witkamp, 1963). There seems to be a higher level of decomposition in 1968. This is probably related to the consistently high humidity during that year; in 1968 much more rain fell during the vegetation season than in 1969 (see table 2). In 1969 the difference in the average rate of decomposition between JC and PL is less. In that year the conditions in JC fluctuated greatly; considerable desiccation as well as stagnation of rain-water took place.

It is not known which invertebrates play a role in decomposition processes and to what extent. The invertebrate populations differ greatly during the season, as is described by De Smidt (1972).

During the first months of the growing season the amount of dead material which disintegrates is greater than the amount which is added as a result of the mortality of the green material ($h_i < x_i$). Before the maximum amount of living biomass is reached, only very little of this material dies (cf. also table 11 and 15 in Chapter IV). In 1968 mortality and decomposition in JC were almost equal, until in October mortality greatly exceeded decay. In 1969 the processes of mortality and decomposition are less parallel during the season. In PL the increase in dead material is initially less than its disintegration; after July, however, h_i is greater than x_i. These results are in complete agreement with those of the changes in standing crop as discussed in Chapter IV (tables 10, 14 and 19). In order to investigate whether or not it was correctly assumed that the growth and mortality of the plants are not influenced by the presence or absence of dead material, a double experiment would have been necessary. This would have involved using new model plots for each new time interval, as did

Łomnicki et al. (1968). This was not done, however, but at the end of the experiment (in October) the amount of green material of the model plots was compared with the yield of green parts from the adjacent plots. No definite conclusion, however, could be drawn. Half the samples of the model plots had slightly less green material than the bordering plots, and the other half contained the same amounts of living parts. During the season no striking changes in the vegetation of the model plots was noted.

The curves showing the increase in living material are very similar. The maximum increase in green parts occurs in May and June, as was to be expected judging from the results of Chapter IV. A re-growth was observed in both vegetations in 1969 during the September-October period. The negative values for y_i in the same period of time in 1968 are presumably due to the fact that the interval of 1 month between the harvests of h_i was too long; so the newly-formed dead material had already disappeared during the same period in which it was formed. Smaller values for h_i were now found than for the decrease in living material. The production figure of JC and PL in 1968 may, as a result of this, be too low. In 1969, when from August onwards the time interval between the harvests of h was shorter, no negative values for y were found.

As expected, the total net primary production, calculated from the sum of the true increase in living material per time interval [$y = h + (b_1 - b_0)$], is higher than that according to the calculations mentioned in Chapter IV (cf. similar investigations by Wiegert & Evans, 1964; Jankowska, 1967, and Traczyk, 1968). The mortality of green parts during the season is being taken into account in Σy_i; this is not so if only the maximum biomass, or the sum of the maximum values of the various species of the vegetation, are considered as the total production (see detailed description in Chapter IV).

The ways of production calculation according to

$$\Sigma y = \Sigma \left\{ h + (b_1 - b_0) \right\} \text{ or } \Sigma\ (h + \Delta b)\ \text{, and } \Sigma(\Delta a + \Delta b)$$

have much in common. The difference in the results is due to the fact that Δa is not equal to h. As described in Chapter IV the determination of Δa is based on both the old and newly-formed dead material. An increase in dead material, as a result of mortality of green parts, may be reduced or completely dominated by a decrease as a result of decomposition of the old parts. The latter was clearly illustrated in table 15, in which the dynamics of the old and the newly-formed dead material in PL are given separately. The difference in new dead material per time unit in this table can, with a few restrictions (loss of material as a result of decomposition) be compared with h_i of the Wiegert-Evans method. The result of the production determination of PL in 1970, obtained from the sum of the increases in weight in new dead material plus the differ-

ences in living material per time unit (607 g/m^2; see table 24 in Chapter IV), agrees with the results according to the calculation Σy_i in 1968 and 1969 (564 and 553 g/m^2 resp.). The difference with regard to the maximum standing crop is proportionately almost of the same order of magnitude; namely, in 1970 34%, in 1969 39%, in 1968 21%. It has already been noted that the calculation for 1968 is probably too low.

If the paired plot method was to be applied in PM, the production figures would probably fluctuate less with those according to the calculation $\Sigma(\Delta a + \Delta b)$ than is the case in JC and PL. There is only very little dead material from previous years present in PM and there is a gradual increase of dead material during the season as a result of mortality (see also fig.13), so that Δa is a better estimation here of h_i than in JC and PL. Also in PM, however, part of the newly-formed dead material will decompose during the same season in which it is formed and, therefore, is not included in the production calculations.

LITTER-BAG EXPERIMENT

Other values for r_i were to be expected with the litter-bag method than with those calculated from the Wiegert-Evans method (cf. also Wiegert & Evans, 1964; Traczyk, 1968). This can be caused by several factors. In the first place the dead material in the bags differs from the dead plant remains lying in the field in the following ways: a) the material consists originally of green material, which is killed by drying at temperatures of 85°C, therefore it is almost sterile when it is placed in the field; b) the material in the bags is much more compact than in the field. Secondly the bags can be a hindrance to large invertebrates which may play a role in the decomposition processes. Thirdly, the microclimate in the bags will be different than that surrounding them; the latter is especially dependent upon the compactness of the material in the bags and the mesh width of the net. Also the fact that all plant parts on the soil surface were removed before the bags were placed must be mentioned as this influences the micro-environment. All these factors will have a detrimental effect on decomposition, especially at the start of the experiment. This effect is lessened after some time, when the bags are completely assimilated into the vegetation as new stems and leaves grow through the mesh and dead plant remains fall onto the bags and algae develop upon them as in the experiment of 1970-1971. Finally, it should be pointed out that in the litter-bag technique the formula: $\frac{\ln(\overline{W}_0/\overline{W}_1}{t_1 - t_0}$ in which $\overline{W}_0$ and $\overline{W}_1$ are the average amounts of dead material (average contents of 5-10 bags) at the beginning and end of the time interval respectively, has been used as an estimate for the average 'artificial' rate of

decomposition. By this formula the population parameter: $\frac{\ln(\mu_0/\mu_1)}{t_1-t_0}$ is only approximately estimated, with μ_0 = the average amount of dead material (gms) of an hypothetical number of bags covering the area at the beginning of the investigated period; μ_1 = the average amount of dead material (gms) of this hypothetical number of bags at the end of the period; and $t_1 - t_0$ = the time interval in days. Considering the standard errors (SD) $\frac{\ln(\mu_0/\mu_1)}{t_1-t_0}$ is reasonably estimated by the formula used. (Using Taylor's expansion it was shown that second order correction terms could be neglected.) The difference Δ between the parameters 'average (artificial) rate of decomposition' and $\frac{\ln(\mu_0/\mu_1)}{t_1-t_0}$ depends upon differences in the geometric and arithmetic mean of the beginning and end conditions, $\Delta = \bar{r} - \frac{\ln(\mu_0/\mu_1)}{t_1-t_0}$. The differences Δ in the litter-bag experiments are probably not much greater than 0.001, so that by applying the formula $\frac{\ln(\overline{W}_0/\overline{W}_1)}{t_1-t_0}$ the obtained numerical results may be accepted as estimations for the average (artificial) decomposition rate.

The differences between r_i of both methods are less than those found by the other authors (Wiegert & Evans, 1964; Traczyk, 1968). The material of the bags (Dralon net curtain with a relatively large mesh width) probably offers more advantages than the nylon insect screen which is usually used (see also Milner & Hughes, 1968; Kelly et al., 1969). The aeration and humidity are probably better in the Dralon bags.

Used correctly, the litter-bag experiment can supply information about eventual plot dependency on the rate of decomposition. The r-values per bag (per place) for the first period of the experiment are given in table 34. The starting conditions (W_0) have obtained the same value artificially (15.00 g in 1968; 10.00 g in 1970) and the observations over the first time interval can be considered as 'paired', as in the Wiegert-Evans method. The period June-August 1968 could also be calculated per location. Unfortunately in 1968, when the bags were placed in groups on various plots with a large distance between them, a great deal of information about plot dependency was lost, due to the fact that during the collection of the bags no note was made of the original location.

The data in table 34 give rise to the presumption that the rate of decomposition is place dependent. Widely divergent r-values were found in 1968 especially. In 1970 the range of values seems to be smaller, probably because in that year all the bags were placed on a relatively small uniformly covered plot in JC. As a result of this, large local differences in environmental conditions were eliminated. Because only the first period of the experiment can be considered here, care must be taken in drawing conclusions about plot dependency. It is

TABLE 34

Instantaneous rates of decomposition (r), by location, of dead material from mesh bags in *Junco-Caricetum extensae* subass. *blysmetosum rufi* (Values in g/g per day)

Year	Location→	1	2	3	4	5	$\bar{r}_i$	S.E.M.
	Interval↓							
1968	25/5–14/6	0.0054*	0.0089	0.0041	0.0056	0.0055	0.0059	0.0008
	14/6– 9/8	0.0055	0.0049	0.0061	0.0061	0.0055	0.0056	0.0002
	Location→	a	b	c	d	e		
	Interval↓							
1970	20/4–27/5	0.0076	0.0052	0.0075	0.0057	0.0055	0.0063	0.0005

* The absolute error Δr_i of each calculation is 0.0001 and is calculated by first order approach of the function $f(x,y) = \frac{\ln (x/y)}{t_1 - t_0}$.

possible that there is only a difference in the speed with which the material in the bags begins to decompose. In the period June-August 1968 for example, the differences between the r-values are much less.

Briefly, it can be said that the Wiegert-Evans method for determining the rate of decomposition of dead material is very time-consuming, even when the modifications according to Łomnicki et al. (1968) and Jankowska (1968) are applied. A second disadvantage is that in very wet sites such as a salt-marsh area, the method can only be used for a very short period of time, namely from May to October. The litter-bag experiment, on the other hand, is less time-consuming and can be used over longer periods. Both experiments give a good impression of the fluctuations in rate of decomposition during the season. The values calculated for r_i, however, are relative values and the accuracy of the estimations, especially from the Wiegert-Evans method, is not great. The litter-bag experiment, therefore, is preferable also as far as accuracy is concerned. The question still remains, however, whether the 'artificial' rate of decomposition, obtained using the litter-bag technique, is a correct reflection of the natural average rate of decomposition upon which the paired-plot method is based.

Although the data concerning mortality obtained by using the Wiegert-Evans method can at the same time be applied in the calculation of the total net primary production, the production determinations in which the increase in dead material (total dead, or even better only newly-formed) is included, are much simpler to obtain a good estimation of the total primary production.

The total decomposition cycle of dead material in JC and PL, from its existance until its complete disappearance, takes about 2 to 3 years. Plant parts with a high lignin content such as the flowering stalks of *L. vulgare*, *Pl. maritima* and

J. gerardii and the leaves of *Juncus* and *Limonium*, seem to need a period of pre-processing ('maceration', cf. Traczyk, 1968), before actual desintegration begins.

During the growing season decomposition is already taking place in some plant parts formed in that season. This involves the succulent parts, especially when they die off early in the season when there is little crude fibre (ligno-cellulose) present. As the plants become older the crude fibre content increases (see table 28), which makes decomposition more difficult. There is a great increase of dead material in the autumn, some of which is carried away by the flood-water during the winter. If this did not take place, an accumulation of dead material would presumably occur, because the growth rate is not equal to the decomposition rate.

SEASONAL CHANGES IN THE STANDING CROP OF UNDERGROUND PLANT PARTS

Method

Root samples, for research into seasonal variations in the biomass of underground plant parts, were collected using an auger which was provided with an aspirator above the stamp (Schuurman & Goedewagen, 1965). This type of auger is particularly useful in very wet areas. The auger, having a diameter of 7.5 cm, was driven into the ground up to a depth of about 13 cm (length of the stamp). The cylinder of soil was pulled out of the ground and kept in a plastic bag prior to further treatment. In *Junco-Caricetum extensae* subass. *blysmetosum rufi* and *Plantagini-Limonietum*, root samples were taken for three and two years respectively. In each experimental plot, 25 cores were collected with a time interval of 4 to 10 weeks. The samples were taken at random, or whenever they were taken at the same time as the samples of above-ground material, the latter spots were chosen, after all the dead and living plant material had been removed. Ten extra samples were then collected in order to make the series up to 25. In 1970 samples were taken from PL within an area of 50 by 30 m, in a long row with 2 m between each sample. Before the root studies were started, it was noted that the majority of the roots occur in the top layer of the soil. This layer, therefore, was studied in detail. Since 1970, when a better auger became available, the 10-20 cm layer was also studied. Cylinders of soil with a length of 20 cm could be pulled out of the ground with this auger and these were then devided into two parts of 10 cm each. Deeper layers have been studied by Lepoutre & Willems (1969). Some of their results will be mentioned in this text.

Due to the fact that is was impossible to study the root samples immediately after they had been collected, they were deep frozen straight away (−20°C) or, if the samples were very wet, they were first dried for some hours at ± 50°C and then deep frozen (Schuurman & Goedewagen, 1965). Before the sand and silt were washed out from the samples, they were soaked in a solution of sodium pyrophosphate (270 g sodium pyrophosphate to 100 l water, according

to Schuurman & Goedewagen, 1965). This solution peptised the clay particles which are present in large quantities in the upper 6 cm of the layer. After soaking (at least 8 hours) the samples were thoroughly rinsed above a sieve with meshes of ± 0.3 mm and freed from silt and sand. Self-made perlon sieves were used on Terschelling, while a copper gauze sieve was used for washing the samples at the Institute of Soil Fertility in Haren (Groningen). The above-ground plant remains, shell chippings and other impurities were removed with with a pair of tweezers during the washing process. For details about the washing process, readers are referred to Schuurman & Goedewagen (1965). The thus obtained root biomass was dried overnight at a temperature of 85°C and the dry weights were determined to the nearest 0.01 g. An average root weight was calculated and converted into biomass per square metre from the 25 cores. No distinction was made between living and dead roots or between roots, rhizomes, stem bases or humus particles. The total underground organic material was taken. It was assumed that real humus particles were only present in very small quantities. Occasionally, sub-samples of the dried roots were taken and ashed in order to determine the sand content.

During the washing process with both sieves (perlon and copper gauze) it was suspected that the copper sieve allowed more material, such as root hairs, humus particles etc. to pass through it, while the loss of material through the perlon sieve was practically negligible. In order to learn more about the difference in perviousness of both sieves, half the number of samples from 4 sample dates were rinsed over one sieve and half over the other sieve. A total of 50 samples per sieve were rinsed in this way and the results compared. Of these 50 samples, 25 came from JC and 25 from PL.

The total net primary production, the rate of production and the turnover values, were calculated from the changes in the biomass of the underground parts. The turnover value is the ratio between net production and maximum standing crop (Dahlman & Kucera, 1965).

No samples were taken from PM for root investigations as, due to the presence of a lot of silt in the soil, the treating of samples by the available apparatus appeared to be impossible.

Results

THE DIFFERENCE IN MESH WIDTH OF THE SIEVE GAUZES

The differences in the amount of biomass from 100 samples washed over sieves made from perlon gauze and copper gauze respectively are given in table 35.

A noticeable difference in perviousness was shown between the two sieves.

TABLE 35

The differences in perviousness between perlon gauze and copper gauze ($\bar{x}_1$ and $\bar{x}_2$ in gms)

	Perlon gauze		Copper gauze		
	n	$\bar{x}_1$	n	$\bar{x}_2$	$\% \frac{\bar{x}_1}{\bar{x}_2}$
JC-samples	50	6.07	50	4.99	122
PL-samples	49	7.28	51	6.08	120

The copper sieve is 20% more pervious. After studying the two sieves more closely, using a microscope, the mesh width of the perlon sieve appeared to be ± 0.30 mm (bought as 0.315 mm mesh width), and that of the copper sieve 0.37 mm, sometimes even more, while it had been assumed that this was also 0.30 mm. In order to be able to compare all the underground production of root material, all calculations for the samples which had been washed over the copper sieve were corrected with regard to the perlon sieve.

SAND CONTENT

The sand content of the root samples from JC and PL was determined for various months. The values are shown in table 36.

TABLE 36

Sand content (in percentages of the total dry weight) of a few root samples from *Junco-Caricetum extensae* subass. *blysmetosum rufi* (JC) and *Plantagini-Limonietum* (PL)

Year	Month	JC	PL
1969	May	3.4	9.2
	September	7.8	3.4
	October	6.9	6.5
	November	6.4	10.2
1970	February	3.1	11.3
	April	1.4	1.7
	May		1.1
	June	1.5	
	July		1.4
	August	1.1	
	September		1.4
	October	1.1	
	December	2.9	2.9

The sand content in JC varied between 1% and 8%; in PL from 1% to 11%. The average amount of sand in PL was somewhat higher than in JC. The values do not differ very much from those found by Schuurman & Goedewagen (1965). Due to the small number of sand determinations made in 1969 and the very low sand content in the samples of 1970, no corrections were made in the calculations of the biomass.

SEASONAL CHANGES IN THE UNDERGROUND BIOMASS

The seasonal changes in the root biomasses of the investigated areas are given in table 37 and in fig.20. The 0-13 cm layer and the 0-10 cm layer can easily be compared with each other because the difference in biomass only amounted to a few percent. This difference is not significant.

Junco-Caricetum extensae subass. blysmetosum rufi

The curves representing the changes in biomass of the three years, are very similar (see fig.20). Minimum values were found in May (1531, 1809 and 1438 g/m^2 resp.); peaks were reached in September-October (2171, 2311 and 1742 g/m^2); after the peak had been reached there was a decrease. In 1968 and 1970 there was a gradual increase from May to October; in 1969 there were more fluctuations in the root biomass. After a decrease in the biomass in the period from April-May, there was an increase until July followed by a decrease, after which a second peak was reached in September. Again a slight increase was observed in the period from October-November. In the autumn of 1969 and 1970 the amount of biomass was almost as much as in the beginning of the year. That was presumably also the case in 1968. If this is true, then the biomass would also have increased somewhat in the early spring of 1968 and 1969.

The 10-20 cm layer showed a slight variation in the biomass. There was a decrease until June, followed by an increase until October. There was only a slight decrease from October to December, until about the same value of standing crop was reached as in the beginning of the year.

Plantagini-Limonietum

The seasonal changes of the root biomasses in PL are similar to those of JC (see table 37 and fig.20). In 1969 an increase in the biomass took place in the period of April-May. A second peak was reached in July, followed by a decrease until September. After a slight increase from September to October, the biomass continued to decrease. In 1970, after a decrease early in the year, the biomass continued to increase over the whole season. A peak in the biomass

TABLE 37

Seasonal changes in biomass of underground plant parts in *Junco-Caricetum extensae* subass. *blysmetosum rufi* (JC) and *Plantagini Limonietum* (PL)

Values in g/m^2 with Coefficients of variation given in brackets.

Site	Year	No.	Sampling dates	Depth in cm			
				0-10(13)		10-20	
JC	1968	1	16/4	2015	(24)		
		2	28/5	1532	(23)		
		3	9/7	1760	(29)		
		4	20/8	1831	(21)		
		5	1/10	2171	(25)		
		6	12/11	1728	(33)		
		7	24/12	1713	(25)		
			average	1836			
	1969	1	4/2	1790	(25)		
		2	24/3	1850	(23)		
		3	16/4	2257	(35)		
		4	14/5	1810	(17)		
		5	10/6	1934	(14)		
		6	8/7	2477	(19)		
		7	5/8	2114	(18)		
		8	2/9	2311	(26)		
		9	6/10	1688	(20)		
		10	12/11	1822	(22)		
			average	2005			
	1970	1	11/2	1635	(16)	226	(27)
		2	1/5	1438	(21)	216	(31)
		3	8/6	1505	(28)	216	(29)
		4	12/8	1589	(25)	257	(38)
		5	1/10	1742	(19)	286	(34)
		6	4/12	1685	(18)	229	(34)
			average	1599		238	
PL	1969	1	23/4	3440	(25)		
		2	21/5	3871	(35)		
		3	17/6	3351	(24)		
		4	15/7	3817	(11)		
		5	12/8	2629	(19)		
		6	10/9	2356	(32)		
		7	8/10	2702	(22)		
		8	20/11	2424	(22)		
			average	3074			
				0-10		10-20	
	1970	1	4/2	2163	(16)	169	(37)
		2	1/5	1581	(31)	125	(34)
		3	27/5	1737	(24)	151	(35)
		4	16/7	2054	(20)	174	(39)
		5	8/9	2220	(25)	182	(29)
		6	7/12	2252	(26)	91	(52)
			average	1970		149	

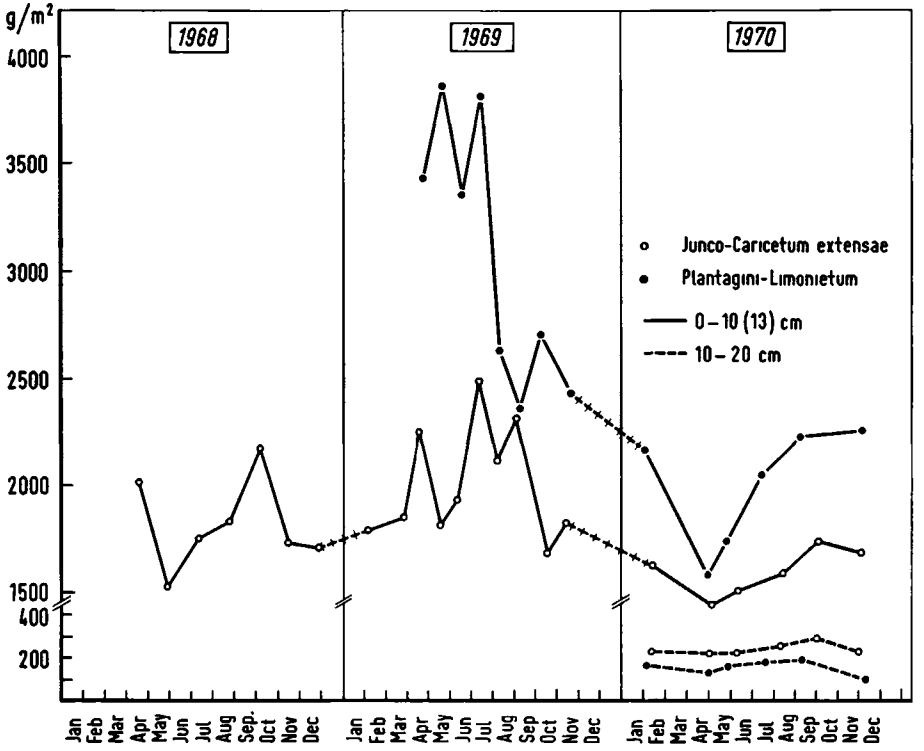

Fig.20. Seasonal changes in underground plant-parts in *Junco-Caricetum extensae* subass. *blysmetosum rufi* and *Plantagini-Limonietum*.

was observed in October-November, but the increase in the autumn was very small. No decrease occurred after the autumn. The roots in the 10-20 cm layer had the same growth dynamics as those in the 0-10 cm layer, except that a noticeable decrease was observed after October. In both vegetation types samples from the 10-20 cm layer show a greater variation proportionally than samples from the top layer.

ROOT DISTRIBUTION OVER THE VARIOUS LAYERS

During investigations into the 0-40 cm soil layer, 80% of the roots was found in the 0-13 cm layer in JC; only 7% of the total biomass was present in the 26-40 cm layer. In PL 85%-90% of the root biomass was found in the 0-13 cm layer and ± 3% in the 26-40 cm layer (Lepoutre & Willems, 1969). Judging from the root distribution over the two layers, it appeared in 1970 also that the roots preferred the top layer. This layer (0-13 cm or 0-10 cm) can be devided into a

silt layer (the uppermost layer) and a layer consisting mainly of sand. The silt layer varies in thickness from 4-6 cm in JC and from 6.5-8 cm in PL. Of the roots which grow in the 0-13 cm layer, 80% were found in the silt layer of JC and 85% in the silt layer of PL. Many of the roots in the silt layer consist of thin, thread-like rootlets.

ROOT PRODUCTION

As a measure of the annual root production, the difference of the biomass was taken between the minimum and maximum values (Dahlman & Kucera, 1965; Kotańska, 1967; Ignatenko et al., 1968; Traczyk, 1968). In 1969 when more than one peak was found, the annual production was also calculated by adding the increases in weight per time interval (cf. Petrusewicz, 1967). The calculated values are given in table 38. It is shown from this that the annual production in the 0-10(13) cm layer in JC varies from 305-790 g/m^2 and in PL from 670-1515 g/m^2. The production in the 10-20 cm layer, in JC 70 g/m^2 and in PL 91 g/m^2, is very small compared with that of the top layer. The highest production of both vegetations was found in 1969. There appears to be a great difference in results when comparing both the production calculations for 1969.

TURNOVER VALUE

TABLE 38

Annual increase in root biomass and root turnover values in *Junco-Caricetum extensae* subass. *blysmetosum rufi* (JC) and *Plantagini-Limonietum* (PL)

Site	Year	Depth in cm	Period with the greatest difference	root biomass in g/m^2			Turnover value
				mini-mum	maxi-mum	annual increase	
JC	1968	0-13	May –Oct.	1532	2171	639	0.29
	1969	0-13	Oct. –July	1688	2477	789	0.59
						(1467)*	(0.32)
	1970	0-10	May –Oct.	1438	1742	304	0.17
		10-20	May –Oct.	216	286	70	0.24
PL	1969	0-13	Sep. –May	2306	3871	1515	0.39
						(1243)	(0.32)
	1970	0.10	May –Dec.	1581	2252	671	0.29
		10-20	Dec. – Sep.	91	182	91	0.50

* The numbers in brackets are the production values, calculated by taking the sum of the increases in the biomass per time interval, and its associated turnover values.

The turnover value, the ratio between the annual production and the maximum standing crop, gives an impression of the total exchange time of the root system. From the data given in table 38 this time can be estimated to be 2-5 years for the roots in JC in the 0-10 cm layer and presumably the same time for the 10-20 cm layer. The exchange time for the underground parts in the top layer of PL is ± 3 years, and in the 10-20 cm layer 2 years.

TABLE 39

Production rates of underground biomass in *Junco-Caricetum extensae* subass. *blysmetosum rufi* (JC) and *Plantagini-Limonietum* (PL). Calculations are based on positive changes in biomass and expressed in $g/m^2/day$.

Site	Year	Sampling period	Number of days in period	Depth in cm	
				0-10(13)	10-20
JC	1968	1-2	42	–*	
		2-3	42	5.42	
		3-4	42	1.70	
		4-5	42	8.09	
		5-6	42	–	
		6-7	42	–	
	1969	1-2	48	1.25	
		2-3	23	17.65	
		3-4	28	–	
		4-5	27	4.62	
		5-6	28	19.41	
		6-7	30	–	
		7-8	28	7.06	
		8-9	34	–	
		9-10	37	3.63	
	1970	1-2	78	–	–
		2-3	38	1.78	–
		3-4	65	1.28	0.64
		4-5	50	3.07	0.57
		5-6	63	–	–
PL	1969	1-2	28	15.41	
		2-3	27	–	
		3-4	28	16.62	
		4-5	28	–	
		5-6	29	–	
		6-7	28	12.37	
		7-8	45	–	
	1970	1-2	87	–	–
		2-3	26	6.00	1.00
		3-4	50	2.64	0.47
		4-5	54	6.51	0.15
		5-6	90	0.35	–

* – indicates that no increase in biomass took place during this sampling period.

TABLE 40

Root-shoot ratios in *Junco-Caricetum extensae* subass. *blysmetosum rufi* (JC) and *Plantagini-Limonietum* (PL), based on total biomass per m^2

Site	Year	Date	Ratio
JC	1968	16/4	6.24
		28/5	7.66
		9/7	4.57
		20/8	5.07
		1/10	6.14
		12/11	–
		total average	5.94
	1969	16/4	14.47
		14/5	6.58
		10/6	5.67
		8/7	4.06
		5/8	5.53
		2/9	4.32
		total average	5.85
	1970	1/5	9.34
		8/6	3.80
		12/8	3.71
		1/10	4.75
		total average	4.75
PL	1969	23/4	14.00
		21/5	11.07
		17/6	6.77
		15/7	6.55
		12/8	4.06
		10/9	4.58
		8/10	5.52
		total average	6.47
	1970	4/2	–
		1/5	–
		27/5	3.57
		16/7	3.09
		8/9	3.29
		total average	3.52

PRODUCTION RATE

The production rates in $g/m^2/day$, based upon the increase in the biomass per time interval, are given in table 39. In all the years of investigations, a high production rate was found for JC in the second half of the summer and, in 1968 and 1969, also in the middle of the summer. In PL, three periods with a

high rate of production were observed in 1969 (early spring, mid-summer and early-autumn), while in 1970 only two periods were found, one in the middle of spring and one in the second half of the summer. In both biotopes the production rates in 1970 were much lower than in the previous years. In JC the rates for the 10-20 cm layer are fairly constant; in PL the highest value was found in spring.

ROOT-SHOOT RATIO

The root-shoot ratios were calculated from the total amount of organic material (dead and living) per square metre (see table 40). The values used for the above-ground biomass are the same as in tables 10 and 14. The average ratios were calculated by taking the average values of the above-ground and of the underground biomass in the years under consideration. The average ratios for 1968 and 1969 in JC are almost the same, namely 5.70 and 5.85. In other words ± 85% of the plant material is underground and 15% above-ground. In PL, the root-shoot ratio was 6.47 in 1969 and 3.52 in 1970. In PL therefore most of the biomass is also underground (78-87%).

Discussion

The differences in the results from the use of a sieve with copper gauze or with perlon gauze, with almost the same mesh widths, allows the conclusion to be drawn that a standardization of the mesh width is to be recommended, in order to facilitate the comparison of the results of various authors. Various mesh widths are mentioned in literature: 290 μ (Troughton, 1951), 300 μ (Schuurman & Goedewagen, 1965), 500 μ (Kelly et al., 1969; Sims, 1970), ± 1300 μ (Pearson, 1965), 1000 μ (Jakrlová, personal communication), 1200-1700 μ (Bray et al., 1959). Often no mesh width is given (e.g. Wiegert & Evans, 1964; Kotańska, 1967; Jakrlová, 1968; Traczyk, 1968). However, a very slight variation in mesh width, such as in the above-mentioned experiment (table 35), makes a noticeable difference to the results. Another two factors could possibly have played a part in the divergency of the results, namely the material of which the sieve is made, and the difference in water pressure. The small plant parts attach themselves somewhat more easily to perlon gauze than to copper gauze. The difference in water pressure is partly compensated by the duration of the washing process.

The curves concerning the dynamics of the underground biomass of the two experimental plots show the same tendency, in spite of the differences between

the plots as a result of environmental factors and other causes. Considerably more fluctuations can be seen in the root biomass curves for 1969 than in those for 1968 and 1970. This could indicate that frequent sampling is preferable to incidental sampling (a few times per year), even if the phenological stages of the above-ground material are taken into consideration, as proposed by Dahlman & Kucera (1965). This is strengthened by the fact that sampling carried out once a fortnight showed even more fluctuations in root biomass as demonstrated by Lepoutre & Willems (1969).

Although little is known about root growth in natural vegetations, it can be assumed that the root dynamics of the two salt-marsh communities have a great deal in common with the results of investigations carried out in cultivated grassland and in the laboratory (McCarty, 1935; Troughton, 1951, 1957; Brouwer, 1965). An increase in biomass is caused by growth and by the increase in reserve materials (minerals and carbohydrates); a decrease is caused by the using up of reserves and by the death and decay of old roots (Kutschera, 1960; Brouwer, 1965; Tesařová & Úlehlová, 1968). These processes are influenced by many factors and are subject to seasonal variations. The same factors, for example temperature and ground humidity, often influence opposite processes such as growth versus decay.

In the experiments concerning the decomposition of dead parts (see Chapter V), the rate of decay was found to be high in spring and late summer. With a few restrictions the same can be said about root decomposition in the investigated biotopes, because the factors influencing the decay of above-ground parts as well as the decay of roots, are substantially the same (Kuranov, 1961; Tesařová & Úlehlová, 1968; Jacubczyk, 1971). Using this knowledge about growth and decomposition several of the variations in the root biomass in JC and PL can be explained. The decrease in the amount of matter in JC in spring (see fig.20) was caused by the consumption of reserve material (soluble carbohydrates) by the plant during rapid above-ground growth (McCarty, 1935; Troughton, 1951; Brouwer, 1965). Part of the decrease can be explained by the high degree of decomposition of the old roots. When the assimilatory surface (more green parts above-ground) increases, an increase in the root biomass takes place. This increase continues until during the autumn, when the above-ground growth already has ceased.

The decrease in the autumn (1968, 1969 and 1970 in JC, and 1969 in PL) was probably due, at least partly, to the dying off of the old roots and the decay of the dead material. Hardly any decrease in root biomass was observed in the two sites in the autumn of 1970. The transfer of reserve materials from the shoots to the roots apparently continued here until late in the season, while the conditions for root breakdown were not favourable. Attention should be paid to the small increase in the root biomass in both fields in the autumn of 1969,

also occurring as a consequence of the translocation of reserve materials, after a period of renewed growth of the aerial parts (cf. Troughton, 1957; Bray et al., 1959; Kelly et al., 1969).

The peak in the biomass of JC in April 1969 showed root growth in a period when there was little shoot growth, as a result of the low temperatures, while the plants still have a large amount of reserve materials (cf. Brouwer, 1965; Troughton, 1957). The peak in May 1969 in PL was mainly due to sample variation. A number of samples with large roots of *Limonium vulgare* resulted in a high average; in addition there was also a high sand content (see table 36). A decrease in the amount of roots in July-August 1969 can be seen in JC as well as in PL, as a great deal of nutrients are necessary above ground in this period of flowering and fruit setting (cf. McCarty, 1935; Troughton, 1951). In September-October the death and decay of old roots increase, due to the rise in the ground water (increasing soil humidity). The decrease in the root biomass because of decay is usually greater than the increase brought about by the translocation of reserve materials from the shoots to the roots. The decrease in biomass is large from September onwards, particularly in the 10-20 cm layer. There is no root growth in the winter period. A decrease in the biomass is chiefly caused by the consumption of reserves for respiration and, so far as conditions are favourable, by the decomposition of old roots.

The method by which the production is calculated is commonly used (Dahlman & Kucera, 1965; Kotańska, 1967; Ignatenko et al., 1968), but the production figures obtained (table 38) are only an approximation of the true production. The annual production is probably underestimated because the death and decomposition of the old roots have not been considered in the calculations. Moreover in 1968 and 1970 the time interval was too large between two harvests; so it is not known whether the minimum and maximum values were really obtained at the time of sampling. In 1969, when sampling was regularly carried out, more than one peak was found in the biomass. From the sum of the increases in weight in JC a production value was obtained which was almost 100% higher than the difference between the minimum and maximum value. This was not the case in PL, but here the first harvest came much later in the season with the result that a possible increase in April did not come to light. In both fields the increase in the amount of underground material in 1970 was noticeably less than in 1969. This could be caused by the difference in weather and site conditions. At the end of April in 1970 there was an unusually high flood which even inundated JC. The flood-water there stagnated as usual. This flood was followed by a dry period lasting for two months. The salinity in the upper layer increased due to evaporation of the water (see also fig.8). This may have influenced root growth troughout the growing season. First the flood and than the dry period may both have caused the large mortality of the thin

fibrous roots (cf. Kutschera, 1960; Weaver & Clements, 1938). This dying off and decay of the small roots may have exceeded the real root growth. During prolonged flooding such as can take place in PL, root growth may be slowed down or even stopped, not only because of a lack of oxygen but also by the toxic effect of the increased CO_2-content (cf. Clements, 1921).

The root biomasses are much larger in PL than in JC, which can be explained by the difference in floristic composition of both sites and the local environmental conditions which result in this different species composition. Taxa occur in PL which have especially thick, fleshy and often lignified roots, such as *Plantago maritima* and *Limonium vulgare. Juncus gerardii* and *Scirpus rufus*, important species in JC have on the other hand, rhizomes and thin, less fleshy roots (see Lepoutre & Willems, 1969). The more fluctuating water economy in PL contributes to the occurrence of such root types.

The values computed for the net annual production in both communities (table 38) are of the same magnitude as the series of values which are known for other types of grassland (Bray, 1963; Pearson, 1965; Kotańska, 1967; Traczyk, 1968). It is, however, difficult to compare the values directly with each other, as the ways in which the roots were obtained often differed greatly. The curves which reproduce the variations in root biomass (fig.20) and the annual increase agree very well with the data from a xerothermic grassland (Kotańska, 1967). This is not so surprising if a salt-marsh is considered as a dry (i.e. physiologically dry) habitat. As a consequence of the high salinity, the absorption of water and ions is more difficult and there is, therefore, an extensive root system necessary (see also elsewhere in the discussion).

The turnover values (table 38) do not noticeably deviate from those of the root systems of natural grassland mentioned by other authors. Dahlman & Kucera (1965) gave 4 years for the total root system of a prairie vegetation, Kotańska (1967) stated 3-4 years for the roots in the top layer (0-5 cm) of some dry grassland communities and 2 years for those in the 5-30 cm layer, and Ignatenko et al. (1968) mentioned an average of 2½ years for the total root system of a lowgrass-herbaceous community, but different times for each separate layer. The differences in turnover values which were found during the 3 years of investigations, are due to the fact that the degree of decay of the underground parts is not the same every year, and this can also be different for each species. Finally, it must be mentioned that the turnover of roots can be different from that of the rhizomes (see also Dahlman & Kucera, 1965).

The distribution of the underground plant parts shows the same pattern as that mentioned in literature. A decrease in biomass occurs with increasing depth (cf. Weaver & Zink, 1945; Troughton, 1951; Kotańska, 1967; Kelly et al., 1969; Van Dyne, 1970). The very high root content in the 0-5 cm layer (80% in JC and 85% in PL of the total contained in the 0-13 cm layer) and

rooting to a depth of only ± 40 cm, are worth mentioning. Many factors such as humidity, oxygen content, temperature, and distribution of minerals in the soil, influence root distribution and the shape of the root system (cf. Kutschera, 1960; Van Donselaar-Ten Bokkel Huinink, 1966). In the salt-marshes, aeration and soil humidity appear to be the most important factors. The frequent fluctuations of the relatively high water level (see Chapter III) which result in a continuously high moisture content of the soil, impede the penetration of the roots to deeper layers because of the prevalent lack of oxygen (Cannon, 1918, 1924; Clements, 1921; Sperry, 1935; Kutschera, 1960). Aeration is optimum in the top layer, this can be seen from its colour which is greyish brown (oxydation layer, containing Fe_2O_3). In a non-aerated situation the colour of this more silt-holding layer is blue-black (reduction layer, containing FeS), as can be seen on the top layer of bare, often flooded areas. Beeftink (1965) also stated that in salt-marsh basins 80% of the roots appeared in the 0-30 cm layer, with 8% air in the upper 8 cm. In creek-banks, with better aeration (10-12% air in the top layer), 80% of the roots were found in the 0-60(70) cm layer. Chapman (1960) mentioned similar values for salt-marsh communities. The somewhat more favourable soil conditions in JC (less silt in the top layer, a less fluctuating water level and no inundation by flood-water during the growing season) result in a slightly deeper root system. The root distribution over the various soil layers in JC also differs from that of PL. A detailed investigation into root penetration and root structure of the diverse taxa, will offer more information about the adaptation of plants to extreme living conditions.

During the years of investigations, a large root production rate was found in late summer in JC, after the maximum shoot growth was completed. This could be caused by continued root growth or by the transport of reserve materials from the stems to the roots (McCarty, 1935; Bray et al., 1959). High values were also found in the period May-July, whenever good growth conditions were present for maximum shoot-growth (high temperatures and low water level). The surplus of materials, formed by the closed plant coverage during the assimilation process, is carried to the roots and used for growth (Brouwer, 1965). The slow growth in the 10-20 cm layer makes it obvious that there is little root expansion under the 10 cm layer. The thick top-layer and the constant high soil humidity below 10 cm impedes the growth.

The high growth rate in the spring of 1969 shows that the conditions for root growth were already favourable at that time, before the start of above-ground growth (see also Brouwer, 1965; Kelly et al., 1969). In PL in 1969 3 periods of high daily production could be observed, namely spring, mid-summer and autumn. These are the periods in which the plants deposit reserve materials in the roots (Troughton, 1957). In 1970 these periods were less clear. As already

stated, root growth may be slowed down after flooding in April, but also the time intervals between the collecting of the samples may have been too great; so less fluctuations were observed. It is uncertain whether or not root growth in all layers follows the same pattern as in the top layer. The results of root studies, carried out by Dahlman & Kucera (1965), Kotańska (1967) and Lepoutre & Willems (1969), show that a considerable difference can exist in the root dynamics in each soil layer.

The root-shoot ratios vary in proportion to the change in development of the underground and above-ground parts. Low values were found in the middle of the summer during the time of maximum shoot biomass; high values appear in spring, when root growth precedes shoot growth, and in autumn when the roots contain a maximum of deposited reserve materials. Root growth and development cannot be considered without correlation with shoot growth and development. Changes in external conditions which influence root growth and mortality will also influence shoot growth. This explains the difference between the average root-shoot ratios during the three years (cf. Bray, 1963). The high root-shoot ratios are very remarkable. Similar high values are usually found in dry regions of the temperate zones, where 80%-90% of the total biomass is present underground (Pearson, 1965; Kotańska, 1967). In damp areas 50%-60% of the total biomass of the plants is to be found underground (see e.g. Wiegert & Evans, 1964), while in communities of floating water plants the roots have practically no share in the total biomass. In salt-marsh communities, as described here, which have a water economy somewhere between the two last mentioned environments, the root-shoot ratio does not fit into this series. The high root-shoot ratios might therefore indicate the dry (in this case physiologically dry) environment. Similar high root-shoot ratios were, however, found by Jakrlová (1971) in meadow communities which were regularly inundated by fresh water. It can perhaps be concluded from this that the excess of water (as found in salt-marsh communities and in the sites mentioned by Jakrlová) makes the presence of a large root biomass necessary, not for water uptake, but for oxygen uptake which is made difficult during inundation. Finally, it is also possible that a large root biomass is not primarily used as an absorption organ, but is necessary for the anchoring of the vegetation.

To summarize, the conclusion can be reached that the shape of the root systems of the two investigated salt-marsh associations are determined by a complex of external factors. The high moisture content of the soil and the changing water level, resulting in bad aeration with a low oxygen supply, lead to a superficial root system. The salinity of the soil and groundwater and the low content of nutrients in the sandy layer, cause extensive root development with numerous side-roots in the upper silt layer (see Kutschera, 1960). The fresh water (rain-water) and nutrients necessary for growth activity of the roots

and shoots, and for photosynthesis, can be acquired in this way. As shown in Chapter III, this silt layer also has a noticeably higher content of organic material and minerals, compared with the underlying sandy layers. The silt layer itself is also a factor which prevents deeper rooting, partly because the layers underneath are badly aerated and partly because no rain-water can filter through as a result of the large amount of roots in this silt layer (cf. Van Donselaar-Ten Bokkel Huinink, 1966). In JC the situation is further complicated because the differences in both the salinity of the soil-moisture and the soil-water level can be even more extreme, but fluctuate less in the time.

Little can be said about the root system of PM because no samples were taken. As stated elsewhere, PM can be seen as the grazed form of PL. Compared with research in other communities it can be expected that the total root biomass in PM is much smaller than that of PL, due to the effect of grazing (Weaver,1950; 1958; Schuster, 1964). *Puccinellia maritima*, the most important species in PM, has a much less extensive root system with few thick, fleshy roots, while the root systems of the *Plantago maritima* and *Limonium vulgare* plants in PM will probably be smaller than those of the same plants in PL. According to Weaver (1950) the effect of grazing is to be found in the replacement of the plant species already present by others having a less extensive root system. The roots in PM also fail to penetrate as far as those in PL; this is partly due to grazing (Schuster, 1964), but also partly due to the thicker silt layer (± 10 cm), which prevents penetration to deeper layers. Roots are scarcely found in the 20-40 cm layer of PM. Root growth could be limited because of the decrease in the assimilatory surface by grazing (Brouwer, 1965), and because of the limited supply of nutrients and water, caused by the less extensive root system (Schuster, 1964). Weaver & Darland (1949) give a survey about the effects of cutting on root production, and they noticed that cutting as a simulation of grazing may eventually cause a decrease in production. In contrast, root growth may also be stimulated by grazing, because manure is added to the area. The difference in species composition in PM compared with PL may also cause a higher rate of growth. Similar results were found by Pearson (1965) who investigated the production of desert plants in grazed and ungrazed vegetation areas. More research is, however, advisable in order to gain a better understanding of root growth in the grazed area.

EFFICIENCY IN THE USE OF SOLAR ENERGY

Method

Solar energy was measured since February 1968 using a solarimeter CM 2/3 manufactured by Kipp & Sons of Delft, the Netherlands. The solarimeter was connected to an integrator CC 1-681 with two counting mechanisms (Kipp & Sons, 1967). The counter switched over automatically from one to the other at 24.00 hours, so that the daily solar radiation could be measured by taking readings from the daily stand of one of the counters. The measured radiation is composed of direct solar radiation and scattered radiation. The measured values were converted into gcal/cm^2. The solarimeter was placed on a flat roof of a bungalow in Midsland-Noord (see fig.1), about 12 km from the experimental plots.

The efficiency of the annual production of the various studied plots, in relation to the total amount of solar radiation, was calculated for the years 1968, 1969 and 1970. The dry weights of the biomasses per square metre were converted into cal/m^2, assuming, on the basis of data found in literature, that 1 g dry weight of grassland material is equivalent to 4000 cal (Odum, 1959; Smalley, 1960; Bray et al., 1959; Golley, 1961; Wiegert & Evans, 1964; Jankowska, 1967). The efficiency was calculated by dividing these converted values by the total radiation, also expressed in cal/m^2. The derived values are given as percentages. As far as above-ground production of JC and PL, in 1968 and 1969 is concerned, production figures obtained from the experiment concerning mortality and decomposition (tables 30 and 31) were used for the efficiency calculations.

For 1970 the maximum standing crop of JC and PL, increased by 25%, was taken as the production figure for the efficiency calculation. This correction of 25% was applied in view of the results of the mortality study. For PM, the sum of the maximum values of the different species in the various years was used as the production figure (column 4 of table 23). The values used for root production in JC and PL were those given in table 38 (Chapter VI). As the root productions of PM were not known, it was estimated that the average root

production is 1.5 times that of the above-ground production, assuming that the root production of PM lies between that of JC and PL.

Apart from the annual efficiency for the total production (stems and roots), the output of the above-ground production only was calculated on the basis of 50% of the total radiation during the vegetation season. It should be noted that the spectrum from 4000 to 7000 Å, which can be used for photosynthesis, represents only half of the total radiation. This efficiency calculation, on the basis of aerial growth, is often applied in agriculture (Wassink, 1948, 1959 and 1964). The period from April 1st to October 1st was assumed to be the vegetation season.

Results

The radiation energy for the various years is shown per decade in table 5. Averages from 1969 and 1970 were assumed for January and February 1968. At the same time, the number of hours of sunshine and the average cloudiness, also per decade, are shown. These data were kindly supplied by the K.N.M.I. in De Bilt. They were collected at the weather stations Hoorn-Terschelling and West-Terschelling. The cloudiness is shown on a scale from 0-10, where 0 is clear and 10 is totally overcast.

The incoming radiation is greatest in June, followed by May and July. Two periods can clearly be distinguished, namely April to October with much radiation and October to April, the winter period, with little radiation. There is a clear relationship between the number of hours of sunshine and the total radiation; more hours of sun give more radiation.

The calculated efficiency percentages are given in table 41. The annual values in PL differ more than in JC mainly due to fluctuations in root production. As stated previously, the root production figures have probably been underestimated (see Chapter VI), therefore the efficiency percentages could also be on the low side. The highest average value, 0.73%, is found in PL; the lowest, 0.44% in JC. Assuming that the root production in PM is about 1.5 times that of the above-ground production, an efficiency of 0.58% is obtained; about the average of JC and PL.

More constant values per site are found if the efficiencies are calculated on the basis of aerial production and 50% usable radiation. The highest average value, 0.63%, is found in PL, followed by PM with 0.58% and then JC with 0.46%.

TABLE 41

Efficiency in the use of solar energy in three salt-marsh communities

JC = *Junco-Caricetum extensae* subass. *blysmetosum rufi*, PL = *Plantagini-Limonietum*, PM = *Puccinellietum maritimae*

SOLAR-RADIATION kcal/m^2				PRODUCTION								EFFICIENCY	
Year	annual total	total growing season	growing season correction [2]	site	year	shoots		roots		total		total growth annual basis	shoot growth growing season 50% usable light
						g/m^2	kcal/m^2	g/m^2	kcal/m^2	g/m^2	kcal/m^2		
1968	(864300)[1]	675390	337695	JC	1968	350	1400	640	2560	990	3960	0.46	0 42
1969	896780	720930	360465		1969	460	1840	790	3160	1250	5000	0.56	0.52
1970	906750	718240	359120		1970	410	1640	305	1220	715	2860	0.31	0.46
average	901760[3]	704850	352425		average	406	1624	578	2312	984	3936	0.44	0.46
				PL	1968	560	2240	–	–	–	–	–	0.66
					1969	552	2208	1515	6060	2067	8268	0.92	0.62
					1970	565	2224	670	2680	1235	4940	0.55	0.62
					average	559	2226	1092	4368	1651	6604	0.73	0.63
				PM	1968	454	1816	–	–	–	–	–	0.54
					1969	512	2048	–	–	–	–	–	0.56
					1970	556	2224	–	–	–	–	–	0.62
					average	507	2028	(760)	(3040)	(1267)	(5068)	(0.56)	0.58

1) estimated value, January and February missing

2) 50% usable light

3) average from 1969 and 1970 values

The largest amount of radiation energy reaches the soil surface in the months of May, June and July (see table 5). These are also the months with the fastest growth (see table 25). There is a clear relationship between the number of hours of sunshine and the amount of radiation, and between the number of hours of sunshine and the average cloudiness. It is more difficult to determine the relationship between the average cloudiness and radiation. Many other factors also play a role in radiation, such as fog and mist, the height, thickness and form of the cloud covering (Van Wijk, 1963; Ångström. 1922) and also the height of the sun (Ångström, 1922).

It is difficult to determine how much scattered radiation forms a part of the total radiation. This can amount to 27% for a clear sky. This percentage is much higher for a cloudy sky (Baas Becking, 1934). The total annual radiation on Terschelling is higher than the average value found for the centre of the Netherlands (e.g. in Wageningen, 51°58′ N., 5°39′ E., Van Wijk, 1963). This is probably explained by the fact that there is more wind on the island and therefore the cloudiness differs from that of the mainland, and that the air is also purer. More radiation can, therefore, reach the surface of the ground. Kimball (1929), who calculated the total solar radiation for the various degrees of latitude, pointed out that the topography of an island can also clearly alter the cloudiness. This also applies presumably to Terschelling; it is often cloudy above the Wadden Sea and/or the North Sea, but not over the island. The opposite can also occur.

The radiation energy found for Terschelling (53° N, 5° E) is similar to the values calculated by Kimball for almost the same degree of latitude, namely 52° N, 10° E (Kimball, 81264 cal/cm^2/year, Terschelling almost 90000 cal/cm^2/year). It is to be recommended that if the radiation cannot be measured in similar investigations as those described in this publication, then Kimball's data should be used.

It can be assumed that the efficiency percentages in the three areas are too low. This is mainly due to the fact that it is difficult to determine a root production figure. Presumably, the estimation of the above-ground production in PM is also too low. It is to be expected that the efficiency is similar to that of PL.

It is difficult to compare the obtained efficiencies with those given in literature. The percentages quoted are often only based on above-ground production; still more often, the radiation values are not given at all in production investigations. The values found for Terschelling do not deviate from the estimation of Rabinowitch, that in natural ecosystems 1% of the total solar energy (= 2% of the usable light energy) is transformed into organic material by the

plants (Rabinowitch, according to Odum, 1959).

Higher efficiences will be found if the gross primary production figures are used in the calculation. More than 50% of the gross production can be used again for respiration by the plants (Odum, 1959). In a salt-marsh vegetation consisting of *Spartina alterniflora*, Teal & Kanwisher (1961) found that the net production only amounted to 23% of the gross production (Teal & Kanwisher, according to Teal, 1962). Teal (1962) calculated an efficiency of 1.4% for this *Spartina* vegetation with a high annual production (6580 kcal/m^2, cf. Smalley, 1959). Data concerning the radiation were taken from Kimball (1929). It was not, however, stated whether the calculation was based on total growth or only on aerial growth. The efficiencies calculated by Bray et al. (1959) vary from 0.04% to 0.53% for the above-ground production of several natural vegetations, and from 0.13% to 0.43% for the total production (stems and roots) of *Zea mays* and *Secale cereale*.

The values given in the last column of table 41 can more easily be compared with those of other investigations, chiefly those concerning agricultural crops. Wassink (1948, 1959, 1964) found that in agricultural crops 1%-2% of the usable solar energy was converted into dry material per vegetation season. The highest value for short periods was found to be 9%. In the laboratory, however, values of up to 20% were found in algae cultures (Wassink, 1959). Efficiencies of 0.46%-0.63%, found for the salt-marshes, agree with the lowest values calculated by Wassink (1948), namely those for onions and carrots. Golley (1960) applied an efficiency calculation, with 50% usable radiation, to the total production of grassland vegetation and found 1.2% efficiency for the gross production and 1.1% for the net production. Transeau (1926), on the other hand, assumed that only 20% of the total radiation is effective for photosynthesis. On this basis his efficiency calculation for maize amounted to 6%.

It is not possible to find a single explanation for the low photosynthetic efficiencies in natural vegetations. Many possible causes are indicated. Wassink (1959, 1964) mentions, for example, too high an intensity of radiation, a too low CO_2 content, too low a temperature, too little humidity, and an incomplete plant coverage ('light-loss' between the plants). There is certainly loss of light during spring, when no closed plant covering is present; especially in PM, where the ground is still completely bare. Maximum coverage does not occur until June. In JC there is also loss of light during the summer. This happens between the upright leaves of *Juncus gerardii* and *Scirpus rufus*. During the growing season, however, a great deal of usable light energy will also be lost in PL and PM during flooding. Only a small part of the radiation can then reach the plants, depending upon the height of the water and its turbidity. This will influence each species of plant differently. Johnson & York (1915), studying the relationship of salt-marsh plants in regard to water levels, presumed that

plants such as *Spartina spec.*, *Suaeda maritima* and *Salicornia europaea* are probably not influenced very much by normal flooding, because often only a relatively small amount of the total daylight is lost, and parts of the plants still remain above the water. During prolonged flooding, photosynthesis will not only be prevented by a shortage of light, but other factors, such as oxygen exchange, will also play a part. Decaying can occur, which leads to a reduction in the green plant parts, and therefore to a reduction in photosynthesis (= production). A more careful investigation is required in order to determine the extent of this loss.

SUMMARY

This publication describes the results of an investigation into the primary production of salt-marsh vegetations. The research was performed within the framework of the International Biological Programme (section PT, 'Productivity Terrestrial') and under the auspices of the Research Institute for Nature Management (until 1969: State Institute for Nature Conservation Research).

It was carried out in the State Nature Reserve 'Boschplaat' on the island of Terschelling, the Boschplaat being one of the few large areas in the Netherlands with a sub-natural landscape.

The field-work took place from 1966 up to and including 1970; 1971 was devoted to processing the results and to a few additional field observations. Aspects of the secondary production were simultaneously studied by other investigators, the results will be published elsewhere.

The problems concerning the research into the primary production were formulated as follows:

How are the investigated plant communities composed and how much organic material, above-ground (leaves, stalks), as well as underground (roots, rhizomes) is periodically produced by these vegetations?

How large are the variations in production per community between the various years, and how great are the differences in production between the various communities?

Are these differences connected with differences observed in a few abiotic factors?

How great is the rate of decomposition of the dead plant material?

How great is the efficiency in the use of solar energy by the communities?

A general description of the Nature Reserve, the Boschplaat, is given in Chapter II. Three associations of the halosere were chosen for investigation: *Junco-Caricetum extensae* subass. *blysmetosum rufi* (JC), of the sand-halosere, and *Plantagini-Limonietum* (PL) and *Puccinellietum maritimae* (PM) of the silt-halosere. PL and PM are physiographically similar vegetations; the difference being of a biotic nature because the former, under the influence of grazing, develops into a *Puccinellietum*. The investigated *Puccinellietum maritimae* is grazed by cattle. The other two vegetation types are ungrazed. The three

associations are situated in the western part of the Boschplaat between km marks 20 and 22 (see fig.1). Fig.2 is a schematic vegetation map of this area. A survey of the nature of the soil of this area is given on the basis of a soil map (fig.3). Finally, a general description of the climate of Terschelling compared with that of the centre of the Netherlands (i.e. De Bilt) is given.

In Chapter III the abiotic factors, which were measured during the years of investigation, are reviewed. As far as the weather is concerned these are, for the years 1967 up to and including 1970, temperature, relative humidity and precipitation (table 2 and figs.4 and 5), cloudiness and the number of hours of sunshine (table 5) and wind direction and velocity (tables 3 and 4 resp.). These meteorological data were obtained from the weather stations of the Royal Netherlands Meteorological Institute, at West-Terschelling and Hoorn-Terschelling.

A few edaphic factors were studied. In 1969 soil analyses were carried out in order to obtain information about the granular composition (fraction rough sand $> 105\ \mu$, fraction fine sand 16-105 μ and the fraction of silt particles $< 16\ \mu$) and the chemical composition (organic material, $CaCO_3$, pH-KCl, P-Al and K-HCl). The results are given in table 6. The soil of PL and PM contains more silt than that of JC and is richer in nutrients. By means of a self-recording tide-meter the water levels of each tide were measured. In this way the flooding frequencies of each biotope could be calculated (table 7.) PM is the most frequently inundated plot and JC the least frequently inundated. The rate of sedimentation is discussed on the basis of data from the literature.

Fig.6 shows the fluctuations of the ground-water level from May 1969 to December 1970. The ground-water level is influenced by precipitation, evaporation and transpiration; in PL and PM to a large extent also by the tidal movement of the water in the closely adjacent creeks.

The moisture content of the various soil layers was determined (table 8 and fig.7), as was the salinity of the soil moisture, expressed in g NaCl/l soil moisture (table 9 and fig.8). The salinity is highest during periods of little precipitation and no floodings. In the top layer (0-5 cm) of JC the salt content varied in 1970 from 7-19 g NaCl/l, in PL from 12-35 g NaCl/l and in PM from 11-54 g NaCl/l.

The changes in biomass of above-ground parts is discussed in Chapter IV. The biomass was determined monthly from April to November. In JC 15 circular samples of 0.125 m^2 were cut per harvest date; in PM the number of samples was 10 each time. The samples were taken from small areas chosen at the beginning of the season, which were surrounded by vegetation cages measuring 4 X 4 m (in 1967 1 X 4 m). In PM 10 samples of 0.125 m^2 were also cut each month from outside these cages, in order to study the influence of grazing on the biomass. The harvested plant material was separated into dead and living

parts; the living material was then sorted into species. Dry weights were determined and the standing crops per m^2 were computed (tables 10, 14 and 19; figs.9, 11 and 13).

The total net primary production was calculated from the changes in standing crop. Table 23 gives the production figures, calculated as maximum standing crop of living material, as the sum of the maximum values of the species separately, as well as the production figures in which the changes in the amount of dead material are included. The total production, calculated according to the latter method, varied in JC from 290-400 g/m^2 (average 340 g/m^2), in PL from 460-550 g/m^2 (average 510 g/m^2), in PM in the enclosures from 390-600 g/m^2 (average 500 g/m^2) and outside the enclosures from 290-450 g/m^2 (average 350 g/m^2).

In JC the production is mainly determined by *Juncus gerardii* and *Plantago maritima*, in PL by *Plantago maritima* and *Limonium vulgare*, in PM by *Puccinellia maritima* and *Salicornia europaea*. These important species may contribute towards 80%-90% of the total production. The difference in production between the years themselves per biotope is, therefore, usually due to changes in biomass of one of these important taxa. The difference in production between the 3 communities can be correlated to the difference in soil properties.

Table 25 gives the production per day for each time interval between two harvests, for the living material as well as for the most important species.

The changes in biomass and floristic composition from a field in PM permanently removed from the effects of grazing (table 26) are also discussed in Chapter IV, as are the production determinations in PM, in which use is made of the movable vegetation cages (table 27). Finally, the results of a few chemical analyses of the plant material are recorded. The contents of crude ash, crude protein and crude fibre were determined (table 28).

The rate of decomposition of dead material in JC and PL is dealt with in Chapter V. Two methods were applied in order to gain an impression of the rate of decomposition during the course of the season, namely the paired-plot method according to Wiegert & Evans (1964) in JC and PL, and the litter-bag technique in JC. On account of the large standard errors (S.E.M.) no significant differences between the rate of decomposition per time interval per biotope were found with the Wiegert-Evans method. However, a tendency was shown towards limited decomposition in dry warm periods (middle summer) and rapid decomposition in spring and autumn. No decomposition occurs during the winter, but some material does disappear from the field due to it being carried away by the flood-water. Production calculations, in which use is made of the data concerning the mortality of the living material during the season, obtained from the Wiegert-Evans experiment, are discussed at some length. The results of these production calculations (table 32) are compared with those given in

Chapter IV.

The changes in biomass of the underground plant parts in JC and PL are examined in Chapter VI. Twenty-five root samples were taken per harvest date using an auger (diameter 7.5 cm); in 1968 and 1969 to a depth of 13 cm and in 1970 to a depth of 20 cm. Incidental samples were taken in 1969 to a depth of 40 cm. The samples were washed over a sieve having a mesh width of ± 0.3 mm. Table 37 and fig.20 give the changes in root biomass. The annual production was calculated from the difference between the maximum and the minimum of the standing crop. When two peaks were present (as in 1969) the total production was also determined by adding the increases in weight per time interval. The root production in JC varied from 300-790 g/m^2, in PL from 670-1515 g/m^2 (table 38). The highest production for both vegetations was found in 1969. The turnover values (the ratio between the annual production and the maximum standing crop) are also given in table 38.

In JC 80% of the roots are found in the upper 10 cm of the soil; in PL up to 90%. Tables 39 and 40 give the production figures per day for each time interval and the root-shoot ratios, respectively. The high root-shoot ratio (JC: 5.94, 5.85 and 4.75; PL: 6.47 and 3.52) indicates in this case a physiologically dry environment.

Finally, the efficiencies of the use of solar radiation (measured with a Kipp solarimeter) are calculated. This was carried out for the total production (above-ground and underground) as well as for the above-ground production alone, on the basis of total radiation, and of 50% of the radiation during the vegetation season respectively. The calculations are given in table 41 of Chapter VII. The results are compared with those of other investigators.

SAMENVATTING

Deze publicatie beschrijft de resultaten van een onderzoek over de primaire productie van kweldervegetaties. Het onderzoek werd verricht in het kader van het Internationaal Biologisch Programma (sectie PT, Productiviteit Terrestrische levensgemeenschappen) en stond onder auspiciën van het Rijksinstituut voor Natuurbeheer (tot 1969: Rijksinstituut voor Veldbiologisch Onderzoek ten behoeve van het Natuurbehoud).

Het onderzoek werd verricht in het Staatsnatuurreservaat 'de Boschplaat' op het eiland Terschelling. De Boschplaat is een van de weinige grote gebieden in Nederland met een nagenoeg natuurlijk landschap.

Van 1966 tot en met 1970 werd het veldwerk uitgevoerd; 1971 werd besteed aan het uitwerken van de resultaten en aan enkele aanvullende veldwaarnemingen. Door andere onderzoekers werden in deze jaren aspecten van de secundaire productie bestudeerd. De resultaten hiervan zullen elders gepubliceerd worden.

De probleemstellingen bij het onderzoek naar de primaire productie waren als volgt geformuleerd:

Hoe zijn de onderzochte plantengemeenschappen samengesteld en hoeveel organisch materiaal, zowel bovengronds (bladeren, stengels) als ondergronds (wortels, rhizomen) wordt periodiek door deze vegetaties geproduceerd?

Hoe groot zijn de variaties in productie per vegetatie tussen de verschillende jaren en hoe groot zijn de verschillen in productie tussen de vegetaties onderling?

Zijn deze verschillen in verband te brengen met waargenomen verschillen in enkele abiotische factoren?

Hoe groot is de snelheid van vertering van het dode plantenmateriaal?

Hoe groot is het rendement van de omzetting der lichtenergie door de vegetaties?

Een algemene beschrijving van het natuurreservaat de Boschplaat wordt in hoofdstuk II gegeven. Drie associaties van de haloserie werden als studie-object gekozen: *Junco-Caricetum extensae* subass. *blysmetosum rufi*, (= JC) van de zand-haloserie en het *Plantago-Limonietum* (= PL) en het *Puccinellietum maritiae* (= PM) van de slib-haloserie. PL en PM zijn fysiografisch overeenkomstige

vegetaties. Het verschil is van biotische aard, daar eerstgenoemde vegetatie onder invloed van beweiding in een *Puccinellietum* overgaat. Het onderzochte *Puccinellietum maritimae* wordt door vee beweid. De specimina der beide andere vegetatietypen waren onbeweid. De drie associaties zijn gelegen in het westelijk deel van de Boschplaat tussen km paal 20 en km paal 22 (zie fig.1). Fig.2 biedt een schematische vegetatiekaart van dit deel. Aan de hand van een bodemkaart (fig.3) wordt een overzicht van de bodemgesteldheid van dit deel gegeven. Tenslotte volgt een algemene beschrijving van het klimaat van Terschelling vergeleken met dat van het binnenland (i.c. De Bilt).

In hoofdstuk III wordt een overzicht gegeven van de abiotische factoren, die gedurende de jaren van onderzoek gemeten zijn. Wat het weer betreft, zijn dit voor de jaren 1967 tot en met 1970: temperatuur, relatieve vochtigheid en neerslag (tabel 2 en fig.4 en 5) en verder bewolking en uren zonneschijn (tabel 5) en windrichting en windsnelheid (tabel 3 en 4 resp.). Deze meteorologische data werden ontleend aan de weerstations West-Terschelling en Hoorn-Terschelling van het K.N.M.I..

Enkele edafische factoren werden bestudeerd. In 1969 werden bodemanalyses uitgevoerd voor de granulaire samenstelling (fractie grof zand $> 105\ \mu$, fractie fijn zand 16-105 μ en de fractie afslibbaar $< 16\ \mu$) en de chemische samenstelling (organisch materiaal, $CaCO_3$, pH-KCl, P-Al en K-HCl). De resultaten staan in tabel 6. De bodem van PL en PM bevat meer slib dan die van JC en is rijker aan voedingsstoffen.

Met behulp van een zelfregistrerende getijmeter werden de waterhoogten bij ieder tij gemeten. Hieruit konden de overstromingsfrequenties van ieder biotoop berekend worden (tabel 7). PM wordt het meest frequent geinundeerd, JC het minst. Aan de hand van literatuurgegevens wordt de sedimentatiesnelheid besproken.

Figuur 6 geeft het verloop van de grondwaterstand van mei 1969 tot december 1970. De grondwaterstand wordt beinvloed door de neerslag, de evaporatie en de verdamping; in PL en PM in grote mate ook door de getijbewegingen van het water in de nabijgelegen slenk.

Het vochtgehalte van verschillende bodemlagen werd bepaald (tabel 8 en fig.7), evenals de saliniteit van het bodemvocht, uitgedrukt in g NaCl/l bodemvocht (tabel 9 en fig.8). In perioden van weinig neerslag en geen overstromingen is de saliniteit het hoogst. In de toplaag (0-5 cm) van JC varieerde het zoutgehalte in 1970 van 7-19 g NaCl/l, in PL van 12-35 g NaCl/l en in PM van 11-54 g NaCl/l.

In hoofdstuk IV worden de veranderingen in biomassa van bovengrondse delen besproken. Van april tot november werd de biomassa maandelijks bepaald. In JC werden per oogstdatum 15 cirkelvormige monsters à 0.125 m^2 geknipt; in PM bedroeg het aantal monsters 10 per keer. De monsters werden

genomen van aan het begin van het seizoen gekozen veldjes, die begrensd werden met een vegetatiekooi van 4 X 4 m (in 1967 1 X 4 m). In PM werden iedere maand ook 10 monsters à 0.125 m^2 buiten deze kooien geknipt, om de invloed van het grazen op de biomassa te bestuderen. Het geoogste plantenmateriaal werd gescheiden in dode en levende delen; het levende materiaal werd vervolgens naar species gesorteerd. Drooggewichten werden bepaald en de standing crop per m^2 berekend (tabellen 10, 14 en 19; fig.9, 11 en 13).

Uit de veranderingen in standing crop werd de totale netto primaire productie berekend. In tabel 23 staan de productiecijfers aangegeven, berekend als maximum standing crop van het levende materiaal, als de som van de maximale waarden van de species afzonderlijk en als de som van de toename in dood materiaal plus het verschil in levend materiaal per tijdsinterval. De totale productie berekend op laatstgenoemde manier varieerde in JC van 290-400 g/m^2 (gemiddeld 340 g/m^2) in PL van 460-550 g/m^2 (gemiddeld 510 g/m^2) in PM in de kooien van 390-600 g/m^2 (gemiddeld 500 g/m^2) en buiten de kooien van 290-450 g/m^2 (gemiddeld 350 g/m^2).

In JC wordt de productie vooral bepaald door *Juncus gerardii* en *Plantago maritima*, in PL door *Plantago maritima* en *Limonium vulgare*, in PM door *Puccinellia maritima* en *Salicornia europaea*. Deze belangrijke soorten kunnen voor 80-90% deel uitmaken van de totale productie. Het verschil in productie tussen de jaren onderling per biotoop is derhalve meestal terug te voeren op veranderingen in biomassa van een van deze belangrijke taxa. Het verschil in produktie tussen de 3 vegetaties is te correleren met het verschil in bodemeigenschappen.

Tabel 25 geeft de productie per dag voor ieder tijdsinterval tussen twee oogsten, zowel van het totale levende materiaal als van de belangrijkste species.

In hoofdstuk IV komen verder nog ter sprake de veranderingen in biomassa en in soortensamenstelling van een permanent uit de beweiding genomen veld van PM (tabel 26) en productiebepalingen in PM waarbij gebruik gemaakt is van verplaatsbare vegetatiekooien (tabel 27). Tenslotte worden de resultaten van enkele chemische analyses van het plantenmateriaal vermeld. De gehaltes aan ruwe as, ruw eiwit en ruwe celstof werden bepaald (tabel 28).

In hoofdstuk V wordt de verteringsgraad van dood materiaal van JC en PL behandeld. Twee methoden werden toegepast om een indruk te krijgen over de mate van vertering in de loop van het seizoen, n.l. de paired-plot-methode volgens Wiegert & Evans (1964) in JC en PL en de 'zakjesproef' in JC. Wegens de grote standaardfouten (S.E.M.) werden met de Wiegert-Evans-methode geen significante verschillen tussen de verteringsgraden per tijdsinterval per biotoop gevonden. Er bleek wel een neiging aanwezig te zijn tot geringe vertering in droge warme perioden (midden zomer) en een snelle vertering in voor- en najaar. In de winter vindt geen vertering plaats, maar er verdwijnt wel materiaal

uit het veld, omdat dit meegenomen wordt met het vloedwater. Uitvoerig wordt ingegaan op de productieberekeningen, waarbij gebruik wordt gemaakt van de gegevens betreffende de mortaliteit van het levende materiaal gedurende het seizoen, die bij het Wiegert-Evans experiment verkregen werden. De resultaten van deze productieberekeningen (tabel 32) worden vergeleken met die in hoofdstuk IV.

De veranderingen in biomassa van de ondergrondse plantendelen in JC en PL staan vermeld in hoofdstuk VI. Per oogstdatum werden met behulp van een boor (diameter 7.5 cm) 25 wortelmonsters genomen; in 1968 en 1969 tot een diepte van 13 cm, in 1970 tot 20 cm. Incidenteel werd in 1969 tot een diepte van 40 cm gemonsterd. De monsters werden gespoeld boven een zeef met maaswijdte van ca. 0.3 mm. Tabel 37 en fig.20 geven de veranderingen in wortelbiomassa. De jaarlijkse productie werd berekend als het verschil tussen het maximum en het minimum van de standing crop. Wanneer twee pieken aanwezig waren (zoals in 1969) werd de totale productie ook bepaald door de gewichtsvermeerderingen per tijdsinterval bij elkaar op te tellen. De wortelproductie in JC varieerde van 300-790 g/m^2, in PL van 670-1515 g/m^2 (tabel 38). In beide vegetaties werd de hoogste productie in 1969 gevonden. Ook de turnover-waarden (de verhouding van de jaarlijkse productie tot de maximale standing crop) staan in tabel 38 vermeld.

In JC bevindt zich 80% van de wortels in de bovenste 10 cm van de grond; in PL tot 90%. In tabel 39 en 40 staan respectievelijk de productiecijfers per dag voor ieder tijdsinterval en de wortel-spruit-verhoudingen. De hoge wortel-spruit-verhoudingen (JC: 5.94, 5.85 en 4.75; PL: 6.47 en 3.52) wijzen in casu op een fysiologisch droog milieu.

Tenslotte zijn berekend de rendementen van de stralingsenergie (gemeten met een Kipp solarimeter). Dit geschiedde zowel voor de totale productie (boven- en ondergronds) als voor de bovengrondse productie alleen, respectievelijk van de totale straling en van 50% van de straling gedurende het vegetatieseizoen. De berekeningen staan in tabel 41 van hoofdstuk VII. De resultaten worden vergeleken met die van andere onderzoekers.

REFERENCES

Adams, D A 1963 Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology **44** 445-456

Adriani, M J. 1945 Sur la phytosociologie, la synécologie et le bilan d'eau de halophytes Groningen

Alberda, Th 1968-1971. Verslagen van het onderzoek PPF 2, IBP section PP – photosynthesis. Mimeographed reports, Inst Biol Scheik Onderz Landb Gewassen, Wageningen

Ångstrom, A 1922. Note on the relation between time of sunshine and cloudiness in Stockholm, 1908-1920 Arkiv fur Matematik, Astronomi och Fisik **17** (15)

Anonymous 1966 Suggested definitions of more import concepts in productivity studies Mimeo Polish Acad Sci

Baas Becking, L G M. 1934. Geobiologie of Inleiding tot de milieukunde Den Haag

Barkman, J J 1959. Phytosociology and ecology of cryptogamic epiphytes Assen

Beeftink, W G 1965. De zoutvegetatie van Z W. Nederland beschouwd in Europees verband Meded.Landb.hogesch Wageningen **65**-1 1-167

Beeftink, W G 1966. Vegetation and habitat of the salt marshes and beach plants in the south-western part of the Netherlands Wentia **15** 83-108

Beeftink, W G. 1968 Die Systematik der Europaische Salzpflanzengesellschaften Ber Int Symp Pflanzensoziol Syst Stolzenau/Weser 1964 239-263

Blaisdell, J P 1958 Seasonal development and yield of native plants on the upper Snake River plains and their relation to certain climatic factors U S Dept Agric Techn Bull 1190. Washington, D C

Blum, J.L. 1968. Salt marsh Spartinas and associated Algae Ecol Monogr **38** 199-221

Bolen, E G 1964. Plant ecology of spring-fed salt marshes in Western Utah Ecol Monogr **34** 143-166

Boorman, L.A. 1971. Studies in salt marsh ecology with special reference to the genus Limonium J.Ecol **59** 103-120

Boyd, C.E. 1970. Production, mineral accumulation and pigment concentrations in Typha latifolia and Scirpus americanus. Ecology **51** 285-290

Braak, C. 1950 Het klimaat van Nederland, Servire's Encyclopaedie, Den Haag

Braun-Blanquet, J. 1928 Pflanzensoziologie. 1.Aufl

Braun-Blanquet, J. 1951. Pflanzensoziologie. 2.Aufl Wien

Braun-Blanquet, J 1964. Pflanzensoziologie 3.Aufl Wien and New York

Bray, J.R. 1962. The primary productivity of vegetation in Central Minnesota USA and its

relationship to chlorophyl content and albedo. In: Lieth, 1962: 102-108

Bray, J.R. 1963. Root production and the estimation of net productivity. Canad.J.Bot. **41**: 65-72

Bray, J.R., D.B. Lawrence & L.C. Pearson. 1959. Primary production in some Minnesota terrestrial communities for 1957. Oikos **10**: 38-49

Brereton, A.J. 1971. The structure of the species populations in the initial stages of the salt marsh succession. J.Ecol. **59**: 321-338

Brouwer, R. 1965. Root growth of grasses and cereals. Meded.Inst.Biol.Scheik.Onderz. Landb.Gewass. **304**, Wageningen; also in: The growth of cereals and grasses: 153-166. Univ.Nottingham

Cannon, W.A. 1918. Root growth in desert plants and the oxygen supply of the soil. Carn.Inst.Wash.Yearb. **17**: 81-83

Cannon, W.A. 1924. A note on the relation of root growth in the soil to the oxygen supply: The growth ratio. Ecology **5**: 319-321

Chapman, V.J. 1960. Salt marshes and salt deserts of the world. New York

Christides, B.G. 1931. The importance of the shape of plots in field experimentation. J. Agric.Sci. **21**: 14-37

Coupland, R.T. & G.M. Van Dyne (ed.). 1970. Grassland ecosystems: Reviews of research (Proc.Sept. 1969 Meeting PT Grasslands Working Group, Intern.Biol.Progr., Saskatoon and Matador, Sask.Canada). Range Sci.Dep.Sci. Ser.No.7, Colo.State Univ., Fort Collins

Cowlishaw, S.J. 1955. The effect of sampling cages on the yield of herbage. J.Brit.Grassl. Soc. **6**: 179-182

Crommelin, R.D. 1940. De herkomst van het zand van de Waddenzee. Tijdschr.Kon.Ned. Aardr.Gen. **57**: 347-361

Dahlman, R.C. & C.L. Kucera. 1965. Root productivity and turnover in native prairie. Ecology **46**: 84-89

Daubenmire, R.F. 1940. Exclosure technique in ecology. Ecology **21**: 514-515

Dieren, J.W. van. 1934. Organogene Dünenbildung. Diss. Amsterdam (Ed. Den Haag)

Dilst, F.J.H. van. 1959. Vegetatiekundige studie langs een transect in het Staatsnatuurreservaat de Boschplaat met overgang van nat-zout naar droog-zoet. Report Bot.Mus. and Herb. Utrecht

Donselaar-Ten Bokkel Huinink, W.A.E. van. 1966. Structure, root systems and periodicity of savanna plants and vegetations in Northern Surinam. Wentia **17**: 1-162

Ellenberg, H. (ed.). 1971. Integrated experimental ecology. Methods ans results of ecosystem research in the German Solling project. Berlin

Favejee, J.Ch.L.. 1951. The origin of the 'Wadden' mud. Meded.Landb.hogesch.Wageningen **51-5**: 113-141

Feekes, W. 1936. De ontwikkeling van de natuurlijke vegetatie in de Wieringermeer, de eerste grote droogmakerij van de Zuiderzee. Ned.Kruidk.Arch. **46**: 1-295

Fouw, J.E.L. de. 1962-1963. Een onderzoek naar de verspreiding en patroonvorming van een

aantal plantensoorten op de duintjes van de Boschplaat van Terschelling. Report Bot.Mus.and Herb. Utrecht

Freysen, A.H.J. 1967a. Some observations on the transition-zone between the xerosere and the halosere on the Boschplaat (Terschelling, Netherlands) with special attention to Centaurium vulgare Rafn. Acta Bot.Neerl. **15**: 668-682

Freysen, A.H.J.. 1967b. A field study on the ecology of Centaurium vulgare Rafn. Diss. Utrecht.

Freysen, A.H.J. & H.T.A. van Heusden. 1965. Festuca rubra on Terschelling. Gorteria **2**: 154-158

Glopper, R.J. de. 1967. Bodemgesteldheid van het Waddengebied. Waddenbull. **2**: 7-11

Golley, F.B. 1960. Energy dynamics of a food chain of an Old-Field community. Ecol. Monogr. **30**: 187-206

Golley, F.B. 1961. Energy values of ecological materials. Ecology **42**: 581-584

Golley, F.B. & J.B. Gentry. 1965. A comparison of variety and standing crop of vegetation on a one-year and a twelve-year abandoned field. Oikos **15**: 185-199

Harper, M.R. 1918. Some dynamic studies of Long Island vegetation. The Plant World **21**: 38-46

Hekstra, G.P. 1965. Internationaal Biologisch Programma. Vakbl.v.Biol. **45**: 94-99

Heukels, H. & S.J. van Ooststroom. 1970. Flora van Nederland. 16th ed. Groningen

Hollmann, A. 1962. Sedimentatie op de Boschplaat. Typewritten report. Fys.Geogr.Inst. Univ. Amsterdam

Hubbard, J.C.E. 1970. Effects of cutting and seed production in Spartina anglica. J.Ecol. **58**: 329-334

Hubbard, J.C.E. & R.E. Stebbings. 1968. Spartina marshes in Southern England. VII Stratigraphy of the Keysworth marsh, Poole Harbour. J.Ecol. **56**: 707-722

Hughes, R.E. 1958. Sheep population and environment in Snowdonia (North Wales). J.Ecol. **46**: 169-189

I.B.P. News, no.1, 1964; no.2, 1965; no.9, 1967; no.10, 1968; no.13, 1969. Issued I.B.P. Secretary, Rome; I.B.P. Central Office, London

Ignatenko, I.V., V.P. Kirillova & V.M. Ponyatovskaya. 1968. The dynamics of plant biomass in lowgrass-herbaceous community. In: Methods of productivity studies in root systems and rhizosphere organisms. Intern.Symp. U.S.S.R. Int.Biol.Prog. U.S.S.R. Acad.Sci.: 68-71

Jagtenberg, W.D.E. & T.A. de Boer. 1957. De bruikbaarheid van graskooien voor opbrengstbepalingen. Landb.Voorlichting **14**: 622-623

Jakrlová, J. 1968. Flooded meadow communities. An analysis of their productivity in a wet year. Folia Geob.et Phytotax. **3**: 345-354

Jakrlová, J. 1971. Flooded meadow communities. An analysis of productivity in a dry year. Folia Geob.et Phytotax. **6**: 1-27

Jakubczyk, H. 1968. Dynamics of microbiological activity in the association Stellario-Deschampsietum on the Strzeleckie meadows in the Kampinos National Park

during the growing season 1965/1966 In Contr Meeting on primary productivity, Cracow, April 1967, 29-42 (mimeographed)

Jakubczyk, H 1969 Dynamics of microbiological activity in some soils of meadow community Report Ecol Inst Polish Acad Sci (mimeographed)

Jakubczyk, H 1971 Productivity investigation of two types of meadows in the Vistula Valley III Decomposition rate of organic matter and microbiological activity Ekologia Polska **XIX** 121-128

Jankowska, K 1967 Sezonowe zmiany roslinosci i produkcja pierwotna netto w płacie łąki Arrhenatheretum elatioris w Ojcowskim Parku Narodowym (Seasonal changes of vegetation and net primary production on a fresh meadow Arrhenatheretum elatioris) Zakład Ochrony Przyrody P A N Studia Naturae Ser A **1** 153-173

Jankowska, K 1968 Methods for the estimation of the disappearance rate of dead plant parts as a basis for estimation of net primary production In Contr Meeting on primary productivity, Cracow, April 1967 14-22 (mimeographed)

Johnson, D S & H H York 1915 The relation of plants to tide levels A study of factors affecting the distribution of marine plants Carn Inst Wash Publ 206

Kelly, J M , P A Ostrup, J S Olson, S J Auerbach & G M Van Dyne 1969 Models of seasonal primary productivity in Eastern Tennessee Festuca and Andropogon ecosystems Oak Ridge Nat Lab ORNL 4310

Kimball, H H 1929 Amount of solar radiation that reaches the surface of the earth on the land and on the sea, and methods by which it is measured Monthly Weather Rev **56** 393-398

Kipp & Sons 1967 Solarimeter integrator CC 1 Direction for use Delft, Netherlands

Kon Ned Meteor Inst De Bilt Maandelijks overzicht der weersgesteldheid **64** (1967), **65** (1968), **66** (1969), **67** (1970)

Kosonen, M 1969 Primary production, composition and seasonal growth rythm of some dry meadow communities on the south coast of Finland Comment Biol Soc Sc Fennica **31** 1-23

Kotanska, M 1967 Biomass dynamics of underground plant organs in some grassland communities of the Ojcow National Park Bull Acad Pol Sci Cl II **XV** 625 631

Krause, W 1960 Ueber das Leistungspotential der Allmendweiden des Hochschwarzwaldes In Lieth, 1962 67-83

Kucera, C L , R C Dahlman & N R Koelling 1967 Total net productivity and turnover on an energy basis for tall grass prairie Ecology **48** 536-541

Kuipers, S H 1962 Bodemkunde Zwolle

Kuranov, V N 1961 Decomposition of plant residues in the soil Soviet Soil Sciences **3** 300-304

Kutschera, L 1960 Wurzelatlas mitteleuropaischer Ackerunkrauter und Kulturpflanzen Frankfurt/M

Leith, H (ed) 1962 Die Stoffproduktion der Pflanzendecke Vortrage und Diskussionsergebnisse des internationalen okologischen Symposiums in Stuttgart-Hohen-

heim 4-7 Mai 1960 Stuttgart

Lepoutre, M W G & G M J Willems 1969 De bepaling van de wortelbiomassa in het Junco Caricetum extensae blysmetosum rufi en het Plantaginl Limonietum op de Boschplaat op Terschelling Report Bot Lab dep Geobotany, Univ Nijmegen

Łomnicki, A & E Bandoła 1967 Szybkosc znikania martwych części roslin jako podstawa oceny produkcji pierwotnej netto (Disappearance rate of dead plant material as a basis for net primary productivity) Zakład Ochrony Przyrody, Polska Akademia Nauk Studia Naturae Seria A 1 19 21

Łomnicki, A , E Bandoła & K Jankowska 1968 Modification of the Wiegert-Evans method for estimation of the net primary production Ecology **49** 147-149

Macfadyan, A 1948 The meaning of productivity in biological systems J Anim Ecol **17** 75-80

McCarty, E C 1935 Seasonal march of carbohydrates in Elymus ambiguus and Muhlen bergia gracilis, and their reaction under moderate grazing use Plant Physiol **10** 727-738

Medwecka-Kornas, A (ed) 1967 Studia ekosystemow lasu bukowego i łąki w Ojcowskim Parku Narodowym (Ecosystem studies in a beach forest and meadow in the Ojców National Park) Zakład Ochrony Przyrody, Polska Akademia Nauk Studia naturae, Seria A 1

Menhinick, E F 1967 Structure, stability and energy flow in plants and arthropods in a Sericea Lespedeza stand Ecol Monogr **37** 255-272

Milner, C & R E Hughes 1968 Methods for the measurement of the primary production of grassland IBP Handbook No 6 Oxford

Miyawaki, A & T Ohba 1965 Studien uber Strand-Salzwiesengesellschaften auf Ost Hokkaido (Japan) Sci Report Yokohama Nat Univ Sec II **12** 1-25

Moir, W H 1969 Steppe communities in the foothills of the Colorado Front Range and their relative productivities Amer Midland Naturalist **81** 331 340

Montalenti, G 1966 The International Biological Programme Penguin Science Survey B 179-188

Moroney, M J 1962 Facts from figures A Pelican Book

Morzer Bruyns, M F & V Westhoff 1951 The Netherlands as an environment for insect life IXth Intern Congr Entom Amsterdam

Mourik, W R van 1968 Dutch I B P programme on small mammals (mimeographed)

Nielsen, N 1935 Eine Methode zur exakten Sedimentationsmessung Kgl Dansk Videns Selsk Biol Meddel **12** 1 97

Numata, M (ed) 1970 Bibliography of grassland ecology in Japan Grassland Project in IBP

Odum, F P 1959 Fundamentals of ecology, 2d ed London-Philadelphia

Odum, E P 1960 Organic production and turnover in old field succession Ecology **41** 34-49

Odum, F P 1963 Ecology Modern Biology Series New York

Odum, E P 1971 Fundamentals of ecology 3d ed Philadelphia London

Odum, E.P. & A.E. Smalley. 1957. Trophic structure and productivity of a salt marsh ecosystem. Progress report Nat.Sci.Foundation. (mimeographed)

Old, S.M. 1969. Microclimates, fire and plant production in an Illinois Prairie. Ecol.Monogr. **39**: 355-384

Ovington, J.D., D. Heitkamp & D.B. Lawrence. 1963. Plant biomass and productivity of prairie, savanna, oakwood and maize field ecosystems in Central Minnesota. Ecology **44**: 52-63

Pearsall, W.H. & E. Gorham. 1956. Production Ecology I. Standing crops of natural vegetation. Oikos **7**: 193-201

Pearson, L.C. 1965. Primary production in grazed and ungrazed desert communities of Eastern Idaho. Ecology **46**: 278-285

Petrusewicz, K. 1967. Concepts in studies on the secondary productivity of terrestrial ecosystems. In: Secondary productivity of terrestrial ecosystems. Proc.Working Meeting IBP-PT. Poland, 1966: 17-51

Ranwell, D.S. 1961. Spartina salt marshes in Southern-England. I. The effect of sheep grazing at the upper limits of Spartina marsh in Bridgewater Bay. J.Ecol. **49**: 325-340

Ranwell, D.S. 1964a. Spartina salt marshes in Southern-England. II. Rate and seasonal pattern of sediment accretion. J.Ecol. **52**: 79-94

Ranwell, D.S. 1964b. Spartina salt marshes in Southern-England. III. Rates of establishment, succession and nutrient supply at Bridgewater Bay, Somerset. J.Ecol. **52**: 95-105

Ranwell, D.S., E.C.F. Bird, J.C.E. Hubbard & R.E. Stebbings. 1964. Spartina salt marshes in Southern-England. V. Tidal submergence and chlorinity in Poole Harbour. J. Ecol. **52**: 627-641

Rawes, M. 1963. The productivity of a Festuca/Agrostis alluvial grassland at 1700 ft. in the Northern Pennines. J.Brit.Grassl.Soc. **18**: 300-309

Rawes, M. & D. Welch. 1966. Further studies on sheep grazing in the Northern Pennines. J.Brit.Grassl.Soc. **21**: 56-61

Richards, F.J. 1934. The salt marshes of Dovey Estuary. IV. The rate of vertical accretion, horizontal extension and sharp erosion. Ann.Bot. **48**: 225-259

Schuster, J.L. 1964. Root development of native plants under three grazing intensities. Ecology **45**: 63-70

Schuurman, J.J. & M.A.J. Goedewagen. 1965. Methods for the examination of root systems and roots. Wageningen

Šestak, Z. & J. Čatský. 1966. Metody studia fotosynthetiké produkce rostlin (Methods of studying photosynthetic production of plants). Academia, Praha

Shanks, R.E. & J.S. Olson. 1961. First-year breakdown of leaf litter in Southern Appalachian forests. Science **134**: 194-195

Sims, P.L. 1970. Studies of producer biomass at the Pawnee Site. In: Coupland & Van Dyne. 1970: 60-61

Smalley, A.E. 1959. The growth cycle of Spartina and its relation to the insect populations

in the marsh Proc.Salt Marsh Conf Mrch.1958, Sapelo Isl Georgia

Smidt, A de. 1972. Aspecten van de algemene en de productie biologie van Phaedon concinnus Steph. en Chrysomela staphylea L. (Coleoptera Chrysomelidae) in het zilte grasland op Terschelling. (in preparation)

Spekman, J. & J Groten. 1963. Enkele aspecten van het Saginetum maritimae op de Beer en de Boschplaat Report Bot Mus.and Herb. Utrecht

Sperry, Th M 1935. Root systems in Illinois prairie Ecology **16** 179-202

Steggewenz, J.H. 1933. De invloed van de getijdebewegingen van zeeen en getijrivieren op de stijghoogte van grondwater Diss Delft

Sterk, A.A. 1968. Een studie van de variabiliteit van Spergularia media en Spergularia marina van Nederland. Diss. Utrecht

Steubing, L. 1965. Pflanzenokologisches Praktikum. Berlin, Hamburg

Stoll, Ph Th. 1965. Een analyse van grondwaterstanden die beinvloed worden door de getijdebewegingen. Meded.Inst Cultuurtech.Waterhuish no 84

Straaten, L M.J U. van. 1954. Composition and structure of recent sediments in the Netherlands Leidse Geol Meded. **19** 1-108

Straaten, L M.J U van. 1959. Origin of recent dutch tidal flat formations Proc Salt Marsh Conf. Mrch.1958, Sapelo Isl Georgia

Sukachev, V.N. & N.V. Dylis. 1966. Programme and methods of biogeocoenological investigations (in Russian) Acad Sci. U S S R. Moscow

Taylor, M.C & E M Burrows. 1968. Studies on the biology of Spartina in the Dee estuary, Cheshire J.Ecol. **56** 795-809

Teal, J.M. 1959. Energy flow in the salt marsh ecosystem Proc Salt Marsh Conf Mrch 1958, Sapelo Isl. Georgia

Teal, J.M 1962. Fnergy flow in the salt marsh ecosystem of Georgia Ecology **43** 614-624

Teal, J.M. 1969. Life and death of the salt marsh. Boston

Teal, J.M & J. Kanwisher. 1961. Gas exchange in a Georgia salt marsh Limnol and Oceanogr. **6** 388-399

Tesařová, M. & B. Úlehlová. 1965. Abbau der Zellulose unter einiger Wiesengesellschaften. D.A.L Tagungsber. **98** 277-287

Tomanek, G W. & F W. Albertson. 1957. Variations in cover, composition, production and roots of vegetation on two prairies in Western Kansas Ecol Monogr **27** 267-281

Traczyk, T. 1968. Studies on the primary production in meadow community Ekologia Polska, Seria A. tom **XVI** 59-100

Traczyk, T. 1971. Production investigation of two types of meadows in the Vistula Valley II. Geobotanical description and primary production. Ekologia Polska, vol **XIX** 93-106

Transeau, C.N. 1926. The accumulation of energy by plants Ohio J Sci **XXVI** 1-10

Troughton, A. 1951. Studies on the roots and storage organs of herbage plants J Brit Grassl Soc. **6** 197-206

Troughton, A. 1957. The underground organs of herbage grasses. Commonw Bur Past &

Field crops. Bull no.44

Tuxen, R 1971. Bibliographia Phytosociologica Syntaxonomica Liefrung 3 Spartinetea, Coeno-Spartinetea. Lehre

Van Dyne, G.M. 1970. Analysis of structure and function of grassland ecosystems A progress report and a continuation proposal. Colorado State Univ Fort Collins

Van Dyne, G.M., W.G. Vogel & H.G. Fisser 1963. Influence of small plot size and shape on range herbage production estimates. Ecology **44** 746-759

Veenstra, H.J. 1971. De herkomst van de Wadafzettingen. Waddenbull. **6** 2-7

Verhoeven, B. 1953. Over de zout- en vochthuishouding van gemundeerde gronden Diss. Wageningen

Verhoeven, B 1962. On the Calciumcarbonate content of young marine sediments Neth J. Agric.Sci. **10** 58-71

Visser, J.C. 1947. De stuifdijken op Vlieland en Terschelling. Tijdschr Kon.Ned Aardr Gen 2e reeks **64** 31-39

Vogl, R.J. 1966. Salt marsh vegetation of Upper Newport Bay, Calif Ecology **47** 80-87

Voisin, A. 1961. Grass productivity. London

Vries, O. de & F.J.A. Dechering 1960. Grondonderzoek 4e druk. Meppel

Wassink, E.C. 1948. De lichtfactor in de photosynthese en zijn relatie tot andere milieufactoren. Meded.Dir Tuinb. **11** 503-513

Wassink, E.C 1959. Efficiency of light energy conversion in plant growth Plant Physiol **34** 356-361

Wassink, E.C. 1964. Rendementen van de omzetting der lichtenergie in laboratoriumproeven en bij de groei van gewassen. Meded.Landb hogesch Wageningen **64**-16 1-33

Weaver, J E. 1950. Effects of intensities of grazing on roots of grasses J.Range Management **3** 100-113

Weaver, J.E. 1958. Summary and interpretation of underground development in natural grassland communities Ecol.Monogr **28** 55-78

Weaver, J E. & F E. Clements. 1938. Plant ecology. 2nd ed. New York-London

Weaver, J E & R W Darland. 1949. Soil root relationships of certain native grasses in various soil types. Ecol.Monogr **19** 303-338

Weaver, J E & E. Zink. 1946. Annual increase of underground materials in three range grasses. Ecology **27** 115-127

Westhoff, V. 1947. De vegetatie der duinen en wadgebieden van Terschelling, Vlieland en Texel. Fotocopy of manuscript diss. Utrecht (Summary of diss. Ed Den Haag)

Westhoff, V. 1949. Schaakspel met de natuur. Natuur en Landschap **3** 54-62

Westhoff, V. 1951. De Boschplaat op Terschelling. Nederlands grootste Staatsnatuurreservaat Natuur en Landschap **5** 1-20

Westhoff, V. 1952. The management of nature reserves in densely populated countries considered from a botanical viewpoint Proc Papers Techn.Meeting I U C N. 77-82. Brussels

Westhoff, V. 1968. Die 'ausgeraumte' Landschaft Biologische Verarmung und Bereicherung

der Kulturlandschaften. In: Handbuch für Landschaftspflege und Naturschutz. Bd. 2: 1-10. München, Basel und Wien

Westhoff, V. 1969. Langjährige Beobachtungen an Aussüssungs-Dauerprobeflächen beweideter und unbeweideter Vegetation an der ehemaligen Zuiderzee. Ber.Int. Symp.Experimentele Pflanzensoziol. Rinteln 1965: 246-255

Westhoff, V. 1970. New criteria for nature reserves. New Scientist **46**: 108-113

Westhoff, V. 1971a. Quelques aspects de la conservation de la nature aux Pays-Bas. Natura Mosana **24**: 33-55

Westhoff, V. 1971b. Choice and management of nature reserves in the Netherlands. Bull. Nat.Plantentuin Belg. **41**: 231-245

Westhoff, V. 1971c. The dynamic structure of plant communities in relation to the objectives of conservation. In: Scientific management of animal and plant communities for conservation. Proc. 11th Symp.Brit.Ecol.Soc.: 3-14. Oxford

Westhoff, V. & G.A. Brouwer. 1951. Rapport inzake de natuurwetenschappelijke betekenis van het Staatsnatuurmonument de Boschplaat op Terschelling. Contact-Comm. Natuur- en Landschapsbescherming. (mimeographed)

Westhoff, V. & S. Segal. 1961. Verslag Cursus Vegetatiekunde 12-17 juni 1961 op Terschelling. Hugo de Vries-lab. Amsterdam. (mimeographed)

Westhoff, V. & C.G. van Leeuwen. 1966. Oekologische und systematische Beziehungen zwischen natürlichen und anthropogenen Vegetation. Ber.Int.Symp. Anthropogene Vegetatione, Stolzenau/Weser: 156-172

Westhoff, V. & A.J. den Held. 1969. Plantengemeenschappen in Nederland. Zutphen

Westhoff, V., P.A. Bakker, C.G. van Leeuwen & E.E. van der Voo. 1970. Wilde planten. Dl.I. Amsterdam

Westlake, D.F. 1963. Comparisons of plant productivity. Biol.Reviews **38**: 385-425

Wetzel, M. 1966. Pflanzenbestand, Nutzung und Futterwert auf Grünland des Norddeutschen Küstenvorlandes. Kali-Briefe. Fachgeb. **4**, 3.Folge: 1-7

Wiegert, R.G. 1962. The selection of an optimum quadrat size for sampling the standing crop of grasses and forbs. Ecology **43**: 125-139

Wiegert, R.G. & F.C. Evans. 1964. Primary production and the disappearance of dead vegetation on an old field in southern Michigan. Ecology **45**: 49-62

Wiehe, P.O. 1935. The effect of submergence by tide on populations of Salicornia europaea. J.Ecol. **23**: 323-333

Wijk, W.R. van (ed.) 1963. Physics of plant environment. Amsterdam

Williams, J.T. 1968. The nitrogen relations and other ecological investigations on wet fertilised meadows. Veröff.Geobot.Inst. E.T.H. Stiftg. Rübel, Zürich **41**: 69-193

Witkamp, M. 1960. Seasonal fluctuations in the fungus flora in mull and mor of an oak forest. Publ.Inst.Biol.Field Res. Arnhem, Neth. **46**: 1-52

Witkamp, M. 1963. Microbial populations of leaf litter in relation to environmental conditions and decomposition. Ecology **44**: 370-377

Witkamp, M. 1966. Decomposition of leaf litter in relation to environment, microflora and

microbial respiration. Ecology **47**: 194-201

Zijpp, A. van der. 1971. Beweiding van de Groede op Terschelling. Report Afd.Natuurb.en Natuurbeh.Landb.hogesch.Wageningen. (mimeographed)

ACKNOWLEDGEMENTS

I wish to express my gratitude to all those who have helped me, in one way or another, to prepare this publication. In particular I should like to mention the following

The Netherlands Organization for the Advancement of Pure Research (Z.W.O.) in The Hague who financed the research.

Dr. J. van Donselaar for his help with the research and for his critical perusal of the manuscript.

All members of the Advisory Committee of the IBP/PT project for the time given to the team on Terschelling.

K. Reinink, my conscientious assistant, for all his help.

My other colleagues on Terschelling, namely W. Dubbeldam W.R. van Mourik and A. de Smidt for the pleasant working relationship.

J.A.M. van Druten of the Computer Centre of the University of Nijmegen for his help with the calculations concerning the rate of decomposition in Chapter V, and for his critical comments on the formulae used in this Chapter and in the literature, and the possible interpretations.

J. Gerritsen, head of the Illustration Department of the University of Nijmegen, for taking care of the drawings.

J.P Ente and J.J. Straat of the Government Department for the IJsselmeerpolders for having the soil surveyed in 1968 and for carrying out the salt analyses in 1970

Dr. J.J. Schuurman of the Institute for Soil Fertility (Haren, Gr) for placing space and material, needed for washing the root samples, at my disposal and for having a few sand determinations carried out.

The Laboratory for Soil and Crop Testing (Oosterbeek) for the analyses of 1967, 1968 (crop analyses) and 1969 (soil analyses).

J. ter Hoeve of the State Forestry Service for the altitude measurements of the experimental plots.

Th. Godding, Mrs. W. van Koten, Mrs. J.M.S. Oostra and Mrs B. van der Hoest, for their help in typing the thesis.

Mrs. P.A Chadwick for translating the manuscript

My wife for her devotion to my work and for her help in correcting the manuscript and the proofs.

By virtue of the graduation laws, article 7, of the Catholic University of Nijmegen, it is forbidden in the thesis to thank any Professor concerned with the University by name

STELLINGEN

I

Vergelijking van de primaire productie van uiteenlopende oecosystemen heeft geen zin, wanneer deze cijfers niet beschouwd worden in de context van gegevens over de milieufactoren waardoor deze oecosystemen bepaald worden.

II

Bij de benaming van pollenzones verdient het aanbeveling de terminologie voor biostratigrafische eenheden in de zin van de code voor stratigrafische nomenclatuur te volgen.

(Code of stratigrafic nomenclature, 1961, Bull.Amer.Ass.Petr.Geol. 45: 645-655)

III

Productie-oecologisch onderzoek in natuurlijke oecosystemen is alleen zinvol in samenhang met structuur-oecologisch onderzoek.

IV

Het is een grote leemte in onze cultuurgeschiedenis dat wij zo weinig weten over de historie van de tuinen van de buitenplaatsen in het Sticht.

V

De 'paired-plot'-methode volgens Wiegert & Evans is een omslachtige en geen nauwkeurige methode voor productie-bepalingen.

(R.G. Wiegert & F.C. Evans, 1964, Ecology 45: 49-64)

VI

Nu de grootte van amfibieën-populaties sterk achteruit gaat is nader oecologisch onderzoek over amfibieën dringend noodzakelijk voor het natuurbehoud, mede omdat zich onder de taxa van deze diergroep waardevolle milieu-indicatoren bevinden.

VII

De grafische methode voor de bestudering van de variabiliteit van plantenmateriaal volgens Jentys-Szaferowa is bij aanwending van electronische rekenmiddelen geschikt voor internationaal gebruik.

(J. Jentys-Szaferowa, 1959, Rev.Pol.Acad.Sci.1 (13): 6-38)

VIII

Het feit dat Tommerup & Ingram nooit het binnendringen van binucleaire zoösporen van *Plasmodiophora brassicae* Woron. in gastheercellen konden waarnemen, zou erop kunnen wijzen dat de verspreiding van deze sporen plaatsvindt door deling van de waardplantcellen.

(J.C. Tommerup & D.S. Ingram, 1971, New Phytol. 70: 327-332)

IX

Bij de waardebepaling van natuurgebieden worden mossen en korstmossen vaak, ten onrechte, niet in de beoordeling betrokken.

X

Bij het invoeren van ingrijpende bezuinigingen inzake subsidies en andere uitgaven voor niet productief te maken takken van Onderwijs, Kunsten en Wetenschappen, dient een Regeering – zelfs in tijden van zeer ongunstige economische conjuncturen – uiterst bedachtzaam te zijn.

(Stelling X, proefschrift F. Ketner, October 1932)

XI

De oprichting van een biologisch station met een vaste staf van medewerkers op een der Wadden-eilanden, naar voorbeeld van 'Weevers' Duin' op Voorne, mag niet langer worden uitgesteld.

XII

Er zal meer aandacht besteed moeten worden aan het beheer van de Boschplaat op Terschelling in verband met zijn status van Europees Natuurreservaat.

XIII

In een subsidie voor onderzoek, verstrekt door de Nederlandse Organisatie voor Zuiver-Wetenschappelijk Onderzoek (Z.W.O.), behoren de kosten van publicatie van dit onderzoek te zijn begrepen, voorzover deze niet door derden gedragen worden. Wanneer de aanvrager zulks niet terstond in zijn begroting opneemt, dient Z.W.O. hem hierop te wijzen en het opnemen van een desbetreffende begrotingspost als voorwaarde te stellen.

22 september 1972 P. Ketner